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THE MATHEMATICS OF BIRD POPULATION GROWTH AND DECLINE

BY R. CAPILDEO AND J. B. S. HALDANE

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It is often desired to calculate the rate at which a closed population would increase or decrease, if its fertility and mortality remained constant at given values. Such calculations can be used for several purposes, for example to see whether mortalities and fertilities derived from observation are compatible with the fact that the population is nearly stationary, or to see whether an observed increase can be explained without immigration. The calculation is always possible, but may be difficult. It is easy (and will be further simplified by the tables given) in the case of organisms for which the following postulates hold:

(1) There is an annual breeding season, so that the organisms can be divided sharply into those hatched or born in particular years.

(2) The mortality of females, after the first year of life, is independent of age.

(3) The fertility of adults is independent of their age.

(4) All members of the species become adult at the same age.

(1) is clearly true for all or almost all wild birds. (2) has been shown by Lack (1950) and others, e.g. Haldane (1953), to be true for many species. (3) is not conclusively proved, but there seems to be no temporal trend in clutch sizes of the same pair of birds observed in successive years. (4) is probably nearly true for most bird species. In most small birds the age is 1 year. Where the age is variable the mathematics are not greatly complicated, provided the percentages maturing at given ages are known. We shall first assume that all birds of a species mature at a years, that the fraction surviving from one year to the next, after the first, is s, and that the net fertility is measured as follows. If N adult females produce so many eggs that fsN of their female progeny are alive at the time of laying in the next year, then f is the *net fertility*. This is less than half the mean clutch size per female (including females not laying) because the mortality in the first year is much higher than in later years. If c is the mean number of eggs laid per year, k the fraction of eggs which not merely hatch but from which the chick survives for 1 year, and if the sex ratio is equality, then $f=ck/2s$, so f is always less than $\frac{1}{2}c$. This somewhat roundabout measure of fertility greatly simplifies the calculations. A similar measure could be made if it were found that, in a long-lived species, the mortality in the years before maturity were not constant. In the case of a bird maturing at a years, we can calculate the number of adults if the annual adult mortality is $(1-s)$, while the fertility and mortality of eggs and young birds are such that, on an average, fs^a female progency per adult female per year reach the age of maturity a.

The value of a is 1 for small birds, and the highest value reported is 9 for *Diomedea epomophora* (Fisher 1952, p. 465). He takes $a=7$ for *Fulmarus glacialis glacialis* (Fisher 1952, p. 358). It is perhaps rather unlikely to be constant. Values of 2, 3 and 4 seem to be commoner (e.g. 4 for *Sula bassana*).

Now consider the dynamics of a population. We denote the number of adult females alive in an area at the start of the breeding season in year n as A_n. Thus for the fulmars of Britain (apart from St Kilda) A_{1950} was about 70,000 (Fisher 1952). These produce sfA_n female progeny alive in the year $n+1$, s^2fA_n alive in year $n+2$, and so on. In the year $n+a$ the s^afA_n survivors become adult, and join the sA_{n-1} adults surviving from year $n-1$ to form A_{n+a}. So

$$A_{n+a}=sA_{n+a-1}+s^afA_n. \tag{1}$$

For example, in a species taking 3 years to mature, so that $a=3$,

$$A_{1953}=sA_{1952}+s^3fA_{1950}.$$

From equation (1) we can calculate the adult populations forwards or backwards in time, provided that the values of A_n are known over a series of a years. In fact, the only number accurately known in most cases is the number of nests occupied, which is somewhat less than A_n, though probably very little less in some species. It can, however, easily be shown that the total population P_n in any calendar date in the year n also follows equation (1) provided death-rates are the same in both sexes.

We desire to find a general expression for A_n or P_n as a function of n. Equation (1) clearly has an infinite number of solutions, depending both on the total number and the age composition of the original population. If $A_n=f_1(n)$, and $A_n=f_2(n)$ are any two solutions of equation (1), then $A_n=bf_1(n)+cf_2(n)$ is a solution, where b and c are any constants. If $A_n=B\lambda^n$ is a solution, equation (1) becomes

$$B\lambda^{n+a}-sB\lambda^{n+a-1}-s^afB\lambda^n=0,$$

whence

$$\lambda^a-s\lambda^{a-1}-s^af=0. \tag{2}$$

This equation has a roots, all different. One and only one is real and positive. If a is even, one is real and negative. The remaining roots are complex. If we call these roots $\lambda_1, \lambda_2, \ldots, \lambda_a$, then

$$A_n=B_1\lambda_1^n+B_2\lambda_2^n+\ldots+B_a\lambda_a^n \tag{3}$$

is clearly a solution, and has been shown to be the complete solution. The values of B_1, B_2, etc., depend on the initial population.

λ_1 is real and positive, so the first term represents stability if $\lambda_1=1$, and otherwise an increasing or decreasing geometrical progression. The other terms represent oscillations round it, which gradually die down.

We first ask what is the condition that the population should settle down to a steady state. This is the condition that $\lambda_1=1$, namely

$$f=\frac{1-s}{s^a}. \tag{4}$$

This equation must hold good for any species in equilibrium, and even if a species increases in numbers for some centuries because f exceeds this equilibrium value, it must finally settle down to it, by a reduction of s, f, or both. Of course, f can be reduced either by a fall in the gross fertility or by a rise in the mortality during the first year.

The equation (3) is most easily solved by putting $\lambda=sx$, when it becomes

$$x^a-x^{a-1}-f=0. \tag{5}$$

We shall first consider what happens when birds mature at 1 or 2 years.

SMALL BIRDS

If $a=1$, equation (3) has only one root $\lambda=(1+f)\,s$, and the population increases or decreases in a geometrical progression according as this exceeds or falls short of unity. For equilibrium, $(1+f)\,s$ must be unity. Let us take an example from the work of Lack & Schifferli (1948). The clutch number of British starlings (*Sturnus vulgaris*) averages about 6, but almost one-quarter of the birds lay a second clutch, bringing the average up to 7·5, so the gross fertility is 3·75. However, the average number of nestlings ringed per breeding pair was 4·65. This is certainly too high, as it does not allow for nests totally destroyed. Of 4789 nestlings ringed, 87 were recovered in later years, as compared with 151 out of 4854 adults. We may assume that $\frac{87}{4789} \div \frac{151}{4854}$ or 0·584 of these nestlings got over the very critical period of learning to fly, after which they had nearly a year's mortality measured by s. This would give a net fertility f of $\frac{1}{2} \times 0{\cdot}584 \times 4{\cdot}65$, or 1·21. Now s is rather accurately known to be 0·494 (annual mortality 50·6 %), so for equilibrium f should be $(1-s)/s$, or 1·02. This is probably near the true value of f, the difference from 1·21 being perhaps due to destruction of 0·19/1·21, or 16 % of the nests, and to non-breeding of some adults.

We see that even in a very well-studied species, though s is known within 2 % or so, f is very poorly known, and the calculated value of 1·02 is certainly nearer the truth than 1·21, or one derived from it by guessing at the percentages of nests destroyed.

BIRDS MATURING AT 2 YEARS

Equation (5) becomes $x^2-x-f=0$. So

$$x=\frac{1\pm\sqrt{(4f+1)}}{2}, \tag{6}$$

whence

$$\lambda_1=\tfrac{1}{2}[1+\sqrt{(4f+1)}]\,s,$$

$$\lambda_2=\tfrac{1}{2}[1-\sqrt{(4f+1)}]\,s=-\frac{[2f+1-\sqrt{(4f+1)}]\,\lambda_1}{2f}.$$

Both are real. They are tabulated in Tables 1 and 2.

The most useful form of the solution of equation (1) is perhaps

$$A_n=\left[\frac{[1+\sqrt{(4f+1)}]\,s}{2}\right]^n\left[B_1+\left\{\frac{\sqrt{(4f+1)}-2f-1}{2f}\right\}^n B_2\right]. \tag{7}$$

If we know the values of A_n in any two consecutive years, say A_0 and A_1, then

$$\left.\begin{aligned} B_1&=\tfrac{1}{2}A_0+\frac{A_1-\frac{1}{2}sA_0}{s\sqrt{(4f+1)}},\\ B_2&=\tfrac{1}{2}A_0-\frac{A_1-\frac{1}{2}sA_0}{s\sqrt{(4f+1)}}.\end{aligned}\right\} \tag{8}$$

For example, if $f=0{\cdot}75$, $s=0{\cdot}7$, equation (6) becomes

$$A_n=1{\cdot}05^n[B_1+(-\tfrac{1}{3})^n\,B_2].$$

That is to say the population increases by 5% per year with a correction factor alternatively positive and negative, decreasing to $\frac{1}{3}$ in each year. And if $A_0 = 100{,}000$, $A_1 = 106{,}000$, then from (7)

$$B_1 = 100{,}714, \quad B_2 = -714,$$

so

$$A_n = (1{\cdot}05)^n \, [100{,}714 - 714(-\tfrac{1}{3})^n].$$

If the population is in equilibrium, so that $f = (1-s)/s^2$ and $\lambda_1 = 1$, then

$$A_n = B_1 + (s-1)^n \, B_2,$$

while

$$B_1 = \frac{(1-s)\,A_0 + A_1}{2-s}, \quad B_2 = \frac{A_0 - A_1}{2-s}.$$

Thus if $f = 0{\cdot}3125$, $s = 0{\cdot}8$, $A_0 = 100{,}000$, $A_1 = 106{,}000$, then

$$A_n = 105{,}000 - (-\tfrac{1}{5})^n \, 5000.$$

BIRDS MATURING AT OVER 2 YEARS

Table 1 gives the value of the real positive root of $x^a - x^{a-1} - f = 0$ for values of a from 2 to 8. It is believed that the range of values of f is adequate. The values of x_1 for intermediate values of f can be obtained by interpolation. For example, if for *Sula bassana* $a = 4$, $s = 0{\cdot}87$ (annual mortality 13%) and $f = 0{\cdot}24$. Table 1 gives $x_1 = 1{\cdot}136$ for $f = 0{\cdot}2$, and $1{\cdot}1818$ for $f = 0{\cdot}3$. So for $f = 0{\cdot}24$,

$$x_1 = 1{\cdot}1363 + 0{\cdot}4(1{\cdot}1363 - 1{\cdot}1818) = 1{\cdot}1545.$$

Table 1. *The real positive root x_1 of $x^a - x^{a-1} = f$*

f	2	3	4	5	6	7	8
0·0	1·0	1·0	1·0	1·0	1·0	1·0	1·0
0·1	1·0916	1·0850	1·0795	1·0749	1·0710	1·0676	1·0645
0·2	1·1708	1·1510	1·1363	1·1249	1·1157	1·1081	1·1016
0·3	1·2416	1·2062	1·1818	1·1636	1·1495	1·1381	1·1286
0·4	1·3062	1·2543	1·2202	1·1957	1·1770	1·1622	1·1502
0·5	1·3660	1·2972	1·2537	1·2233	1·2005	1·1827	1·1683
0·6	1·4220	1·3361	1·2837	1·2476	1·2210	1·2005	1·1840
0·8	1·5247	1·4052	1·3357	1·2894	1·2560	1·2305	1·2103
1·0	1·6180	1·4656	1·3803	1·3247	1·2852	1·2554	1·2321
1·2	1·7042	1·5197	1·4195	1·3555	1·3105	1·2769	1·2507
1·5	1·8229	1·5919	1·4711	1·3955	1·3432	1·3045	1·2745
2·0	2·0000	1·6956	1·5437	1·4511	1·3881	1·3421	1·3070
2·5	2·1583	1·7848	1·6048	1·4973	1·4252	1·3731	1·3335
3·0	2·3028	1·8637	1·6581	1·5372	1·4570	1·3994	1·3560
3·5	2·4365	1·9349	1·7055	1·5725	1·4849	1·4225	1·3756
4·0	2·5616	2·0	1·7484	1·6041	1·5098	1·4430	1·3930
4·5	2·6795	2·0602	1·7877	1·6329	1·5324	1·4616	1·4087
5·0	2·7913	2·1163	1·8240	1·6594	1·5532	1·4786	1·4231

The steady rate of annual increase or decrease is $\lambda_1 = sx_1$.

The steady rate of increase would be $\lambda_1 = sx = 1{\cdot}0044$, so the population, when oscillations had died down, would be increasing by 0·44% annually. The true value of x_1 is 1·1555. To obtain a value accurate within such an error, one would have to count several million birds So the error is negligible.

Table 2 gives the second root $x_2 = -0{\cdot}53594$, so $\lambda_2 = -0{\cdot}4663$. This means that the geometrical progression given by the first root has a correction, alternatively positive and negative, which is reduced each year in a ratio of 0·4663.

Table 2. *The real negative root x_2 of $x^a - x^{a-1} = f$*

	a			
f	2	4	6	8
0·0	0·0	0·0	0·0	0·0
0·1	0·0916	0·4136	0·5761	0·6690
0·2	0·1708	0·5097	0·6553	0·7345
0·3	0·2416	0·5753	0·7063	0·7760
0·4	0·3062	0·6265	0·7448	0·8063
0·5	0·3660	0·6691	0·7761	0·8307
0·6	0·4220	0·7059	0·8025	0·8513
0·8	0·5247	0·7678	0·8460	0·8848
1·0	0·6180	0·8192	0·8813	0·9116
1·2	0·7042	0·8635	0·9111	0·9341
1·5	0·8229	0·9209	0·9490	0·9623
2·0	1·0000	1·0000	1·0000	1·0000
2·5	1·1583	1·0657	1·0414	1·0302
3·0	1·3028	1·1223	1·0764	1·0555
3·5	1·4365	1·1723	1·1068	1·0774
4·0	1·5616	1·2174	1·1339	1·0967
4·5	1·6795	1·2584	1·1588	1·1140
5·0	1·7913	1·2962	1·1805	1·1297

The negative sign is to be prefixed in every case.
Oscillations with a period of 2 years increase or decrease by an annual factor of sx_2.

Table 3 gives x_3 and $x_4 = 0{\cdot}4406(\cos 101{\cdot}03^\circ \pm i \sin 101{\cdot}03^\circ)$. This means that there is another correction with a period of 3·559 years, decreasing by a factor of 0·3823 per year.

Table 3. *Complex roots of $x^3 - x^2 = f$ in the form $r(\cos\theta + i\sin\theta)$*

f	r	θ°	Period
0·0	0·0	90·0	4·0
0·1	0·3063	98·05	3·672
0·2	0·4168	100·43	3·584
0·3	0·4987	101·93	3·532
0·4	0·5648	103·02	3·495
0·5	0·6208	103·85	3·467
0·6	0·6701	104·52	3·444
0·8	0·7546	105·58	3·410
1·0	0·8260	106·37	3·384
1·2	0·8886	107·00	3·364
1·5	0·9707	107·75	3·340
2·0	1·0860	108·68	3·312
2·5	1·1835	109·37	3·292
3·0	1·2688	109·90	3·276
3·5	1·3449	110·33	3·263
4·0	1·4142	110·70	3·252
4·5	1·4779	111·02	3·243
5·0	1·5371	111·29	3·235
∞	∞	120·0	3·0

Angles are given in decimals, not minutes.
The oscillations whose period is given are damped or increased by an annual factor rs.

$A = B_1(1{\cdot}0442)^n + B_2(-0{\cdot}4663)^n + B_3(0{\cdot}4406)^n \cos(101{\cdot}03n^\circ + B_4)$, where B_1, B_2, B_3, B_4 depend on the initial population, and can be calculated if its age composition is known.

Next suppose it is found, with the same values of f and s, that 10 % of birds mature in their third year, 70 % in their fourth, and 20 % in their fifth. We find the values of

x_1 for $a=3$, 4 and 5 as before. They are 1·19912, 1·1545 and 1·14038. We take the weighted average

$$0{\cdot}1 \times 1{\cdot}19912 + 0{\cdot}7 \times 1{\cdot}1545 + 0{\cdot}2 \times 1{\cdot}14038 = 1{\cdot}1561.$$

This is accurate enough. The true value is 1·1533. The value 1·1561 corresponds to an annual increase of 0·94 %. In this case we cannot use Tables 2–4.

Table 4. *Complex roots of* $x^4 - x^3 = f$ *in the form* $r(\cos\theta + i\sin\theta)$

f	r	$\theta°$	Period
0·0	0·0	60·0	6·0
0·1	0·4733	69·33	5·192
0·2	0·5876	71·48	5·036
0·3	0·6643	72·77	4·947
0·4	0·7234	73·70	4·885
0·5	0·7720	74·42	4·838
0·6	0·8137	74·97	4·802
0·8	0·8832	75·83	4·747
1·0	0·9404	76·50	4·706
1·2	0·9895	77·03	4·673
1·5	1·0523	77·66	4·635
2·0	1·1382	78·43	4·590
2·5	1·2090	79·02	4·556
3·0	1·2698	79·47	4·530
3·5	1·3231	79·84	4·509
4·0	1·3709	80·15	4·492
4·5	1·4143	80·40	4·478
5·0	1·4542	80·65	4·464
∞	∞	90·0	4·0

The only case which can be solved quite simply is that when $a=3$, and $f=(1-s)/s^3$, so that the population oscillates round an equilibrium. In this case equation (2) becomes

$$\lambda^3 - s\lambda^2 - 1 + s = 0,$$

so

$$\lambda_1 = 1, \quad \text{or} \quad \tfrac{1}{2}\{-1+s \pm \sqrt{[-(3+s)(1-s)]}\}. \tag{9}$$

The complex roots may be written as $\sqrt{(1-s)}^{(\cos\theta \pm i\sin\theta)}$, where $\cos 2\theta = -\frac{1}{2}(1+s)$, so that $\pi > \theta > \frac{1}{2}\pi$. So the oscillation has a period between 2 and 4 years, and its amplitude is, on an average, decreased by a factor of $1-s$ in every 2 years.

Further details are given in the Appendix.

DISCUSSION

Accurate values of the annual survival, s, are being obtained for a number of species by picking up ringed birds. Accurate data on clutch size also exist. On the other hand, even in so well-studied a species as *Sturnus vulgaris* there is considerable doubt as to the value of the net fertility f, largely through the difficulty of measuring the mortality of eggs, nestlings and fledgelings. It is likely that for many species a more reliable value of f will be obtained from equation (4) than from actual observation. This, however, will not be true for populations like those of *Sula bassana* and *Fulmarus g. glacialis*, which, round Britain at least, are probably far from being in equilibrium.

The hypothesis that annual death-rates and fertility rates are constant is, of course, too simple. They vary considerably from year to year. But the data so far available suggest that on an average they are pretty steady. Any species well adapted to its environment can replenish its numbers within a few years after a disaster. Thus the British

herons were reduced to 53 % of their standard density by the severe winter of 1946–47, but had arisen well above it by 1952 (Nicholson & Alexander 1950 and later). And passerine species, at least, show little tendency to rise above a density which appears to depend on their territorial system.

It seems likely that, when the density falls, the effective fertility f rises. It is likely that when the density is near saturation, many birds find unsuitable nesting places, and, in some species, do not nest at all. When density is lowered by a disaster, it is suggested that the average number of offspring successfully reared increases. There is not much evidence for regulation by disease due to overcrowding among birds with a territorial system, though it certainly occurs among sea birds. But even here there is no evidence for catastrophic effects of overcrowding, such as occur in many insect and some mammalian species. It seems likely that bird populations are mainly regulated by changes in effective fertility which, on our definition, includes the effects of mortality in the first year of life. The data are, however, probably insufficient to make a mathematical theory worth while. The tables given should make calculations such as that of Fisher & Venables (1938) extremely easy, and it is doubtful whether we are yet justified in making more ambitious ones.

SUMMARY

The annual changes in a bird population with constant mortality and fertility can be calculated with the aid of tables here given. Under these conditions a population of a species maturing at 1 year remains steady, or increases or decreases in a geometrical progression. If maturity is postponed for 2 or more years, there are damped oscillations round stability or a geometric progression. The relation between mortality and fertility is calculated in the general case, and some applications to published work are given.

REFERENCES

Fisher, J. (1952). *The fulmar.* London.

Fisher, J. & Venables, L. S. V. (1938). Breeding gannets (*Sula bassana*) on Noss, Shetland, with an analysis of the rate of increase of this species. *J. Anim. Ecol.* **7**, 305–13.

Haldane, J. B. S. (1953). Some animal life tables. *J. Inst. Actu.* **79**, 83–90.

Lack, D. (1950). Population ecology in birds. *Proc. Xth Ornithol. Congr., Uppsala*, pp. 409–48.

Lack, D. & Schifferli, A. (1948). Die Lebensdauer des Stares. *Ornith. Beob.* **45**, 107–14.

Nicholson, E. M. & Alexander, W. B. (1950). An index of heron population. *Brit. Birds*, **54**, 123–6 (and later).

APPENDIX

The tables do not permit the calculation of the real roots when the age of maturity is over 8 years or when f is less than 0·1 or of the complex roots when it is over 4.

When $a=9$ or more, the real roots are readily calculated as follows. If $x^a - x^{a-1} = f$, then so long as f is less than $\frac{(a-1)^{a-1}}{a^a}$, if $b = a-1$,

$$x_1 = 1 + f - bf^2 + \frac{b(3b+1)f^3}{2!} - \frac{b(4b+1)(4b+2)f^4}{3!} + \frac{b(5b+1)(5b+2)(5b+3)f^5}{4!} + \text{etc.} \tag{10}$$

And if $c=1/(a-1)$, $p=f^c$, the real negative root x_2 is given by

$$-x_2=p-cp^2+\frac{c(3c+1)p^3}{2!}-\frac{c(4c+1)(4c+2)p^4}{3!}+\ldots. \tag{11}$$

When an approximate value has been found from one of these series, we can find a better approximation by Newton's method, using the formula

$$x'=x\left[1-\frac{x^a-x^{a-1}-f}{x^{a-1}(ax-a+1)}\right]. \tag{12}$$

In practice it may be simpler to begin with $1+f$, or to guess. Thus if $a=10, f=0{\cdot}07$, we guess $x=1{\cdot}04$. Formula (12) gives 1·0468, and applied to 1·0468 it gives 1·04650, which is accurate to five decimal places. The real negative root is found similarly.

When $a=3$, the complex roots are given by

$$r=\sqrt{\frac{f}{x_1}}, \quad \theta=180^\circ-\cos^{-1}\left(\frac{1-x_1}{2r}\right). \tag{13}$$

When $a=4$, they are given by

$$r=\sqrt{\frac{f}{-x_1x_2}}, \quad \theta=180^\circ-\cos^{-1}\left(\frac{1-x_1-x_2}{2r}\right). \tag{14}$$

These can be used if the value of f is outside the range of the tables, or if very great accuracy is needed. To calculate the complex roots when a exceeds 4, we have

$$r^a\cos a\theta-r^{a-1}\cos(a-1)\theta-f=0,$$
$$r^a\sin a\theta-r^{a-1}\sin(a-1)\theta=0.$$

So

$$\left.\begin{aligned} f&=\left[\frac{\sin(a-1)\theta}{\sin\theta}\right]^{a-1}\left[\frac{\sin a\theta}{\sin\theta}\right]^{-a},\\ r&=\frac{\sin(a-1)\theta}{\sin a\theta}. \end{aligned}\right\} \tag{15}$$

But if $p=a\cos 2\theta$

$$\frac{\sin 4\theta}{\sin\theta}=(2+p)^{\frac{1}{2}}p, \quad \frac{\sin 5\theta}{\sin\theta}=p^2+p-1, \quad \frac{\sin 6\theta}{\sin\theta}=(2+p)^{\frac{1}{2}}(p^2-1),$$

$$\frac{\sin 7\theta}{\sin\theta}=p^3+p^2-2p-1, \quad \frac{\sin 8\theta}{\sin\theta}=(2+p)^{\frac{1}{2}}(p^3-2p), \quad \text{etc.}$$

Hence for $a=5, \theta=\frac{1}{2}\cos^{-1}(\frac{1}{2}p)$, $f=\dfrac{(2+p)^2p^4}{(p^2+p-1)^5}$, $r=\dfrac{(2+p)^{\frac{1}{2}}p}{p^2+p-1}$.

Two values of p correspond to each value of f, and when these are found, the values of r and θ can be calculated. The calculation for higher values of a is similar.

Finally it may be desired to calculate the numerical constants B_r in equation (3). If the values A_0, A_1, etc. are known over a years, we have a simultaneous equations

$$\left.\begin{aligned} B_1 \quad &+B_2 \quad +B_3 \quad +\ldots=A_0,\\ B_1\lambda_1&+B_2\lambda_2+B_3\lambda_3+\ldots=A_1,\\ B_1\lambda_1^2&+B_2\lambda_2^2+B_3\lambda_3^2+\ldots=A_2.\\ &\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \end{aligned}\right\} \tag{16}$$

Hence, in the case where $a=3$,

$$B=\begin{vmatrix} 1 & 1 & A_0 \\ \lambda_2 & \lambda_3 & A_1 \\ \lambda_2^2 & \lambda_3^2 & A_2 \end{vmatrix} \div \begin{vmatrix} 1 & 1 & 1 \\ \lambda_1 & \lambda_2 & \lambda_3 \\ \lambda_1^2 & \lambda_2^2 & \lambda_3^2 \end{vmatrix}$$

$$=\frac{r^2s^2A_0-2rs\cos\theta A_1+A_2}{s^2(x_1^2-2rx_1\cos\theta+r^2)},$$

and similar results for B_2 and B_3. In practice it will usually be simpler to calculate the numbers expected in successive years directly from equation (1).

THE FEEDING HABITS OF SOME OF THE FISHES AND SOME MEMBERS OF THE BOTTOM FAUNA OF LLYN TEGID (BALA LAKE), MERIONETHSHIRE

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(With 3 Figures in the Text)

During recent work on the bottom fauna of Llyn Tegid (Bala Lake) the feeding habits of some of the fish and members of the bottom fauna were investigated with the hope of showing an interrelationship between the fish and the bottom fauna, and between various members of the bottom fauna. The volume of previous work on the subject of fish diets is considerable. Hartley (1947, 1948) investigated the feeding habits of coarse fishes in certain parts of Britain, whilst Allen (1935), Radforth (1940) and Swynnerton & Worthington (1940) have all contributed work in this field. Jones (1949, 1950, 1951) has contributed a valuable series of papers on invertebrate feeding habits, whilst Hynes (1941), Slack (1936) and others have contributed work on the feeding habits of aquatic larvae of various groups of the Insecta.

THE FISHES OF LLYN TEGID

Fish present in Llyn Tegid include:

Grayling	(*Thymallus thymallus* Linn.)	Gudgeon	(*Gobio fluviatilis* Linn.)
Salmon	(*Salmo salar* Linn.)	Bullhead	(*Cottus gobio* Linn.)
Trout	(*S. trutta* Linn.)	Pike	(*Esox lucius* Linn.)
Gwyniad	(*Coregonus pennantii* Cuv. & Val.)	Roach	(*Rutilus rutilus* Linn.)
Perch	(*Perca fluviatilis* Linn.)	Eel	(*Anguilla anguilla* Linn.)
Minnow	(*Phoxinus phoxinus* Linn.)		

I have investigated the feeding habits of gwyniad, perch, pike and roach, and have also examined a very small number of trout and grayling stomachs. All the fish, other than gwyniad, were caught in seine nets near the shore; the gwyniad were taken in gill nets. Perch and roach were taken from late March to September when they were in shallow water. The guts were removed on capture whenever possible; if not the fish were slit open along the ventral surface and preserved in 70% alcohol or 5% formaldehyde. Most fish were measured from the tip of the snout to the fork of the tail.

(*a*) *Perch*

The thirty fish examined could be divided into two groups, with average length of 112 and 185 mm. The fish were caught in June and July 1951. Fig. 1 gives the results of the gut analyses of the fishes. In the smaller fish the main food eaten were Ostracoda, with *Caenis moesta* nymphs second in importance. These two food items were present in most fish, and where present formed the greatest bulk of the gut contents. The

remaining foods were of secondary importance. In the larger fish *Gammarus pulex* formed the main food. One fish had eaten only *Asellus meridianus*. The remaining foods were of secondary importance.

It would appear from the above somewhat scanty data that perch are essentially bottom feeders in the shallow waters which they inhabit during the warmer months, and that the size of the predominant food eaten at this time of the year increases with the size of the fish. Allen (1935) found that fish less than 140 mm. in length ate plankton mainly. This is not in agreement with the findings on the Llyn Tegid perch, which were bottom feeders, the Ostracoda eaten being bottom dwellers and not planktonic. Swynnerton & Worthington (1940), working on Haweswater perch, found that these fish ate *Gammarus*. Hartley (1947) found that perch were bottom feeders, some concentrating on one source of food.

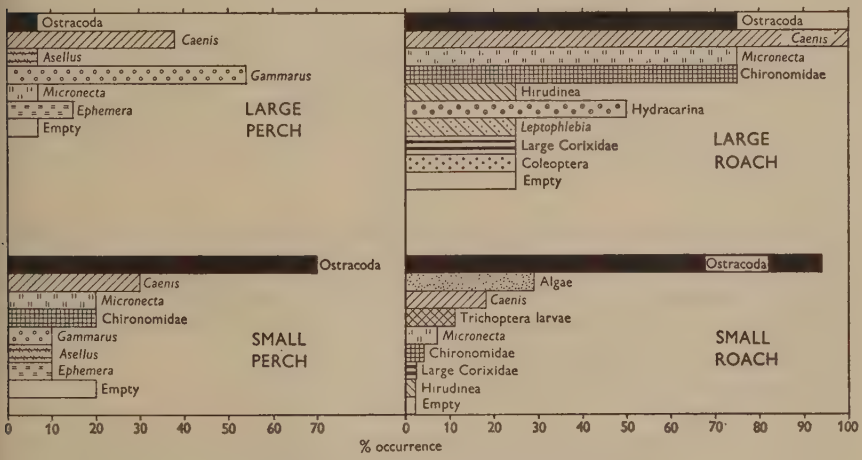

Fig. 1. The food of perch and roach of Llyn Tegid.

(*b*) *Roach*

Fifty roach were taken in June 1951, the majority being small specimens with an average length of 89·9 mm.; five larger specimens averaging 142·25 mm. long were also opened. Fig. 1 shows the food eaten by the different fish with the relative importance of each constituent of the diet. All were feeding on bottom fauna. The smaller roach ate mainly Ostracoda with filamentous algae second in importance. These foods formed the main bulk of the gut contents. Both small roach and small perch ate Ostracoda. The roach differed in taking a fair proportion of algae in addition. Small roach and small perch ate approximately the same proportion of *Caenis moesta*. The larger roach examined had not eaten algae, *C. moesta* nymphs being the commonest food taken. The size of the food eaten increased with size of fish, as seen in perch. The larger roach took a greater variety of food than the small roach.

Hartley (1948) classifies roach of the Cam district as 'fish eating mainly insects and plants'. He finds they 'compete almost directly with the minnow for food but that the food eaten varies in importance with the two fishes'. Table 1 compares the food

of Llyn Tegid and Cam roach. Hartley (1947) discusses the feeding habits of roach, but none of his points is in complete agreement with the data obtained from roach of Llyn Tegid. Planktonic crustacea were never found in Tegid roach, and algae and other plants decreased in importance as a source of food for large roach. Molluscs were never found in the stomachs of roach though they were present in the lake. Though *Gammarus* was present in the lake in large numbers, none was found in any roach stomach.

Generally speaking the Tegid roach ate the same food as the Cam roach, but the relative importance of the main foods eaten differed in the two and seemed to depend on the relative quantity of the foods present on the substratum. Radforth (1940) found that the filamentous algae were the main source of food in Tweed roach, which also took many diatoms. Animal remains were rare.

Table 1. *Main food of roach of Cam district and Tegid*

	Percentage of fish containing foods stated		
Food eaten	Cam (Hartley)	Tegid (small fish)	Tegid (large fish)
Ephemeroptera	2	17·6	100
Orthocladiinae	14·5	4	50

(*c*) *Pike*

These were exclusively fish eating, the smaller specimens (up to 280 mm.) taking mainly minnows and very young roach, perch and trout, and the larger ones taking larger fish including roach, perch, trout, grayling and on seven occasions, a gwyniad. These findings are in agreement with those of Hartley (1948) and others who have stated that pike eat mainly other fishes.

(*d*) *Grayling*

Four grayling stomachs were taken from fish caught in March 1952. Even though only four fish were examined, it may be significant that all four were feeding on the bottom at this time of the year. The dominant food in three stomachs was *Limnea pereger*. *Gammarus pulex* was almost as common in all three fish, being equalled in one of these by *Asellus meridianus*. In all four fish a considerable quantity of bottom grit was also present. Radforth (1940) states that the grayling is 'catholic in its taste for food' and eats food most easily available in its habitat. This appears true of Tegid grayling.

(*e*) *Trout*

Three stomachs from fish taken in March 1952 were examined. The dominant food in all stomachs was *Gammarus pulex*. The small number of stomachs opened does not justify any statement about the general feeding habits of Tegid trout, but the results do agree with those of Swynnerton & Worthington (1940) who found that the Hawes-water trout also fed mainly on bottom insect larvae.

(*f*) *Gwyniad*

Eight specimens were examined, taken singly or in twos at different months throughout the year. The first, caught on 3 July 1951, was 140 mm. in length. Its stomach contained only bottom animals, the main food eaten being *Micronecta poweri*

adults, with *Caenis moesta* nymphs second in importance. *Gammarus pulex* and *Asellus meridianus* were present but were of little importance. The stomachs of two fish taken in February 1952 were empty. A single specimen taken 16 May 1952 was 120 mm. in length. The stomach contents consisted of approximately equal volumes of *Agraylea multipunctata* larvae in their cases, *Tinodes* larvae and Orthocladiinae larvae. Three *Asellus meridianus* and a single *Gammarus pulex* were also present. Two fish taken 13 May 1952, 215 and 223 mm. in length, and two others taken 28 May 1952, 212 and 190 mm. in length, contained planktonic crustacea exclusively. These four fish were caught in gill nets, the others by seine nets.

There are no previous reliable records of feeding habits of this species. From my own analysis it would seem that small fish up to 150 mm. long fed exclusively on the bottom, and this would explain why they were caught in littoral regions by a seine net, which was only 12 ft. deep. Data from the larger fish indicate that they were plankton feeders. Records of feeding habits of other species of white fish are numerous both in British and American literature. The schelly (*Coregonus stigmaticus*) in Haweswater is reported by Swynnerton & Worthington (1940) to feed near the bottom of the lake on Entomostraca. They point out that like the powan (*C. clupeoides*) in Loch Lomond, the schelly may also sometimes feed on the 'true plankton', as it has been seen in shoals at the water surface at night.

THE INVERTEBRATA

Only the commoner members of the Invertebrata of the bottom fauna have been examined for gut contents. It was not possible to determine gut contents of any Hemiptera or Coleoptera, as in all instances the food particles were too small for identification. I have attempted to establish the feeding habits of the species listed below; in each instance fifty specimens were examined except where otherwise indicated.

CRUSTACEA	Amphipoda	*Gammarus pulex* de Geer.
INSECTA	Neuroptera	*Sialis lutaria* Linn.
	Ephemeroptera	*Siphlonurus lacustris* Etn.
		Ephemera danica Müll.
		Leptophlebia marginata Linn.
	Plecoptera	*Nemoura avicularis* Morton.
		Diura bicaudata Linn.
	Trichoptera	*Halesus* sp.
		Sericostoma personatum Spence.
		Polycentropus flavomaculatus Pictet.
		Tinodes waeneri Linn.

(*a*) Gammarus pulex

The *Gammarus* examined were taken from shore stations round the lake and were collected at different times. Fig. 2 shows the foods found within the gut, and their relative importance in the diet. The food is finely divided in the gut, and where present detritus forms the greatest bulk of the food. Diatoms often form a considerable proportion of the gut contents. The occurrence of the spines and mandible of an insect

larva in two specimens seemed to be unusual. It is interesting to note the remarks of Adamstone & Harkness (1923) who report that, except in the Trichoptera and Chironomidae which select their food, the presence of diatoms in the gut of Invertebrata eating detritus is purely accidental. These data agree fairly closely with those of Hynes (personal communication). Jones (1951) reports that *G. zaddachi* in the River Towy fed chiefly on chironomid larvae.

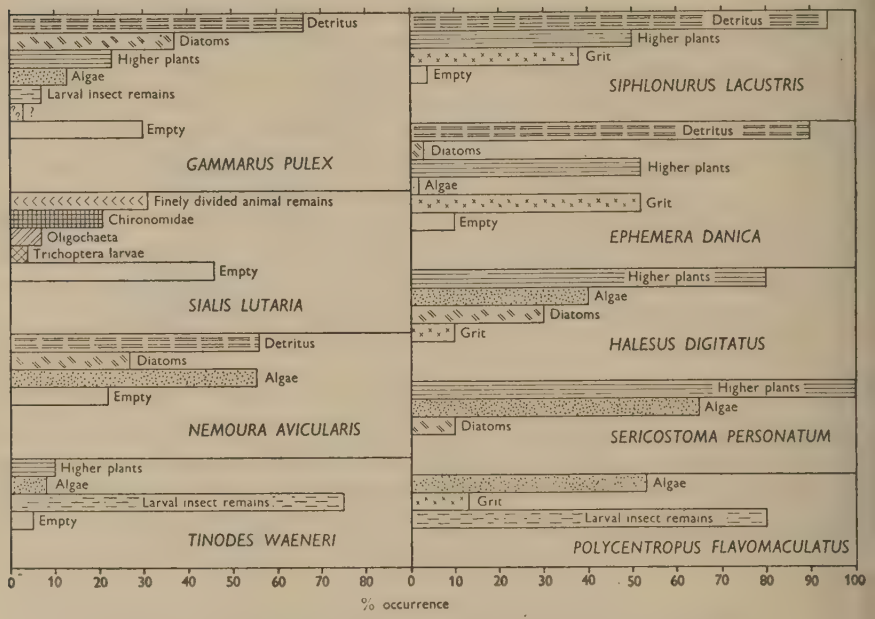

Fig. 2. The food of some invertebrates of the bottom fauna of Llyn Tegid.

(*b*) Sialis lutaria

Of the sixty-seven larvae examined, thirty were empty. The remainder were found to have been exclusively carnivorous. Fig. 2 shows the main food of the larvae. The detritus or amorphous gut contents seen in a large proportion of the larvae examined was invariably present in the hind gut, and was probably of animal origin since no trace of plant material was found in the anterior portion of the gut. There was a marked difference in the food eaten by specimens taken from littoral regions and those from deeper waters (6–12 m.), a difference undoubtedly governed by the decrease in variety of animals with increasing depth. The shore forms eat most of the invertebrate species present in the littoral region, but in deeper water chironomid larvae form the main bulk of the diet.

The gut of *Sialis* larvae is adapted to their carnivorous feeding habits since in the hinder part of the fore gut is an area covered by chitinous teeth which is probably used to help in triturition within the gut.

(*c*) Siphlonurus lacustris

The guts of all twenty specimens taken were examined. Fig. 2 shows the food eaten. The food was entirely of vegetable origin, 93·75% of guts containing mainly detritus. 37·5% contained gritty material probably taken in with the detritus off the substream.

(*d*) Ephemera danica

Forty nymphs were examined. These were taken from a depth of 0–6 m. The food was the same at all depths, and was similar to that of *Siphlonurus lacustris* in that it consisted mainly of detritus (Fig. 2). One nymph contained part of an insect larva, which I was unable to identify. This would not appear to be a usual food in Tegid specimens. Wissmeyer (1926) found that *Ephemera* nymphs ate far more animal food than other ephemeropteran nymphs, this consisting of broken parts of insects, such as hooks and bristles, broken shells, a whole daphnid and a piece of gut with its contents, but he shows that 50–86% of total food was plants and detritus so that vegetable food was dominant.

(*e*) Leptophlebia marginata

Fifty specimens were examined and all contained mainly detritus, with a small percentage of algal filaments and diatoms (Fig. 2). In examining the ephemeropteran gut contents I found that mature larvae were invariably empty, as did Jones (1950) when he examined the gut contents of Ephemeroptera and Plecoptera. In most instances it was possible to see whether or not the gut was full through the body wall of the nymph. Eaton (1883–88), discussing the Ephemeroptera, reports that they 'mostly eat mud or minute aquatic vegetation such as covers stones or plants, but, judging from maxillae and mandibles some must be predacious'. Wissmeyer (1926) found that though some species ate a small amount of animal food, most fed on detritus and plant material. Jones (1949, 1950) states that the common mayflies are wholly herbivorous and that the Ephemeroptera are mainly detritus feeders, but eat algae and higher plants.

It would appear that the feeding habits of the three common ephemerid species found in Tegid are similar to those of other Ephemeridae, as described by previous workers.

(*f*) Nemoura avicularis

Twenty specimens were examined. Fig. 2 shows the percentage occurrence of the foods eaten by the nymphs of this species. Detritus and algae were equally represented, with diatoms present in 16·6% of the specimens examined. These were probably taken in accidentally, not as a result of selection by the nymphs. Hynes (1941) reports that the nymphs ate mostly higher plant material but a few ate algae; this agrees with the data from Llyn Tegid.

(*g*) Diura bicaudata

Only four specimens were obtained; of these, two were empty, and two contained insect larvae and higher plant remains. Hynes (1941) reports that nymphs of this species feed 'largely on animal matter but also eat algae and higher plant tissue'.

(*h*) Halesus digitatus

Twenty-five specimens were examined. Fig. 2 shows the relative importance of different foods. The specimens were exclusively phytophagous, the majority containing fragments of higher plants, diatoms and filamentous algae also being present in some. Slack (1936), investigating the feeding habits of a species of this genus, found it to be exclusively phytophagous. Jones (1950), examining the feeding habits of *H. radiatus*, found algae and fragments of *Glyceria* sp. in the gut.

(*i*) Sericostoma personatum

Fifteen specimens were examined. All specimens were phytophagous, the gut being filled with fragments of higher plants. Ten specimens also contained a small quantity of filamentous algae with diatoms. Jones (1950) found only fragments of higher plants in the gut, together with what appeared to be wood parings. Slack (1936) found that fragments of dead leaves were present in many specimens, and in one instance a cladoceran was present; the food was otherwise like that of *Halesus* sp.

(*j*) Polycentropus flavomaculatus

This species was found to be predominantly carnivorous, 80% containing larval insect remains; 53% contained filamentous algae and 10% contained nothing but grit off the substratum. Jones (1950) found that this species was entirely carnivorous, feeding on a variety of insects. Badcock (1949) reports that the species is carnivorous in the tributaries of the Welsh Dee, 'avoiding algae caught in their nets'. This is not in agreement with my observations where I found that though predominantly insectivorous, the specimens examined also contained a fair proportion of algae. Moon (1934) found that this species in Windermere ate small crustacea.

(*k*) Tinodes waeneri

Twenty specimens were opened and their gut contents examined. The species was almost entirely carnivorous, 75% containing insect larvae remains while only 10 and 7·5% contained filamentous algae and diatoms respectively; 5% of those examined were empty. Wesenberg-Lund (1908) reports that he has observed the larvae of this species eating algae encrusting stones. Berg (1938) suggests that 'the animals build their long tunnels as they creep over the stones, feeding as they go'. The findings of Wesenberg-Lund are not in agreement with those for the larvae of this species living in Llyn Tegid. Hickin (1946) states that campodeiform larvae of the order (e.g. *Tinodes* and *Polycentropus*) differ from the eruciform type (e.g. *Halesus* or *Sericostoma*) in that usually no case is constructed and the larva spins a net attached to the underside of stones. Small insects and crustacea are caught in the web and devoured by the larvae. This statement indicates that caseless larvae are carnivorous whereas cased larvae are vegetarian, and this is supported by observations on specimens from Llyn Tegid. Jones (1949) states that: 'Food of aquatic insects is determined to a considerable extent by the environment in which they live.'

DISCUSSION

A very general picture of the food relationships of the dominant groups of animals in the Lake can now be given. Using the types I have investigated and modifying Rawson's (1930) scheme it is possible to give a clear picture of the food relationships

of the Llyn Tegid fauna. Fig. 3 shows this diagrammatically. The cycles are basically the same as those shown by Rawson, but are further subdivided. It can be seen that the bottom fauna falls into three groups:

(1) those dependent upon aquatic plants for food,
(2) those dependent upon detritus for food, and
(3) those dependent upon groups (1) and (2) for food.

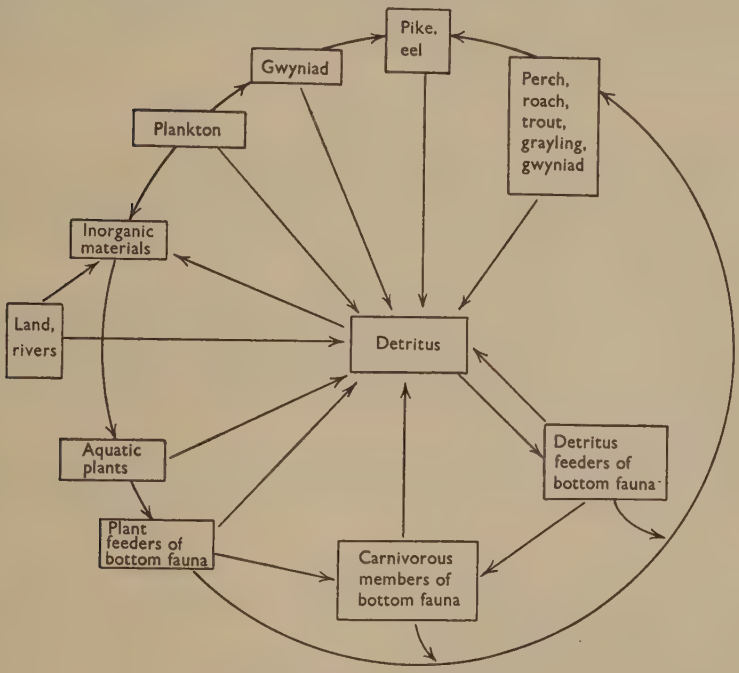

Fig. 3. The food cycle in Llyn Tegid.

Plant feeders	Carnivores	Detritus feeders
Mollusca	*Diura bicaudata*	Oligochaeta
Plecoptera	*Sialis lutaria*	*Asellus meridianus*
Ephemeroptera	Hirudinea	*Gammarus pulex*
Cased Trichoptera	Tanypodinae	*Micronecta poweri*
Littoral Chironomidae	Caseless Trichoptera	Benthic Chironomidae
		Ephemeroptera

Each of these three groups contributes to the detritus of the lake, by decomposition and formation of waste products of excretion as also do the plankton and all the fishes. The fishes similarly fall into three groups:

(1) those dependent on plankton for food,
(2) those dependent on bottom fauna for food, and
(3) those dependent on (1) and (2) for food.

Each of these groups is ultimately dependent on the remaining plant and animal populations of the lake; for example the bottom fauna, which forms food for so many

fish, is in a large part dependent on detritus for food. Each group thus represents a minor cycle which depends for its continuance upon its relationship with the other minor cycles.

ACKNOWLEDGEMENTS

I should like to express my sincere thanks to Drs H. B. N. Hynes and J. W. Jones of the Department of Zoology, University of Liverpool, for their invaluable help in sampling and for criticism of the manuscript, and to the Welsh Land Sub-Commission for permission to work on the Lake; also to Mr J. Boyle, Bailiff to the Welsh Land Sub-Commission, for his help in sampling.

SUMMARY

1. The feeding habits of several species of fish in Llyn Tegid (Bala Lake) are discussed. It was found that the roach, perch, and grayling examined were essentially bottom feeders, whilst gwyniad were bottom feeders only for a part of their lives, becoming plankton feeders as they grew larger. Trout were bottom feeders as far as could be estimated, and pike were piscivorous.

2. Of the invertebrates investigated, the nymphs of Ephemeroptera, and *Gammarus* are essentially detritus feeders. Those Plecoptera nymphs investigated were partially phytophagous and partially detritus feeders. *Sialis lutaria* (Neuroptera) was carnivorous, whilst the Trichoptera examined consisted of some carnivorous and some phytophagous species.

3. A general picture of the food cycle in Llyn Tegid is given. The bottom fauna and the fishes are each divided into three groups, all of which are interdependent.

REFERENCES

Adamstone, F. B. & Harkness, W. J. K. (1923). The bottom organisms of Lake Nipigon. *Publ. Ont. Fish. Res. Lab.* **15**, 123–70.

Allen, K. R. (1935). The food and migration of the perch (*Perca fluviatilis*) in Windermere. *J. Anim. Ecol.* **4**, 264–73.

Badcock, R. M. (1949). Studies in stream life in tributaries of the Welsh Dee. *J. Anim. Ecol.* **18**, 193–208.

Berg, K. (1938). Studies of bottom animals of Esrom Lake. *K. danske vidensk. Selsk.* (Sect. Sci.) (9), **8**.

Eaton, A. E. (1883–88). A revisional monograph of recent Ephemeridae. Parts I–VI. *Trans. Linn. Soc. Lond. (Zool.)* (2), **3**, 1–352.

Hartley, P. H. T. (1947). The natural history of some British freshwater fishes. *Proc. Zool. Soc. Lond.* **117**, 129–206.

Hartley, P. H. T. (1948). Food and feeding relationships in a community of fresh-water fishes. *J. Anim. Ecol.* **17**, 1–13.

Hickin, N. E. (1946). Larvae of the British Trichoptera. *Trans. R. Ent. Soc. Lond.* **97**, 187–212.

Hynes, H. B. N. (1941). The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs. *Trans. R. Ent. Soc. Lond.* **91**, 459–557.

Jones, J. R. E. (1949). A further ecological study of calcareous streams in the 'Black Mountain' district of South Wales. *J. Anim. Ecol.* **18**, 142–59.

Jones, J. R. E. (1950). A further ecological study of the River Rheidol: the food of the common insects of the main-stream. *J. Anim. Ecol.* **19**, 159–74.

Jones, J. R. E. (1951). An ecological study of the River Towy. *J. Anim. Ecol.* **20**, 68–86.

Moon, H. P. (1934). An investigation of the littoral region of Windermere. *J. Anim. Ecol.* **3**, 8–28.

Radforth, I. (1940). The food of the grayling (*Thymallus thymallus*), flounder (*Platichthys flesus*), roach (*Rutilus rutilus*) and gudgeon (*Gobio fluviatilis*), with special reference to the Tweed Watershed. *J. Anim. Ecol.* **9**, 302–18.

Rawson, D. S. (1930). Bottom fauna of Lake Simcoe and its role in the ecology of the lake. *Publ. Ont. Fish. Res. Lab.* **34**, 1–183.

Slack, H. D. (1936). The food of caddis fly (Trichoptera) larvae. *J. Anim. Ecol.* **5**, 105–15.

Swynnerton, G. H. & Worthington, E. B. (1940). Notes on the food of fish in Haweswater (Westmorland). *J. Anim. Ecol.* **9**, 183–7.

Wesenberg-Lund, C. (1908). Die littoralen Tiergesellschaften unserer grösseren Seen. *Int. Rev. Hydrobiol.* **1**, 574.

Wissmeyer, A. (1926). Nahrungsuntersuchungen bei Ephemeriden-Larven. *Arch. Hydrobiol.* **16**, 668–98.

THE LARVAL INHABITANTS OF COW PATS

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(With 7 Figures in the Text)

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INTRODUCTION

It has been recorded for over 200 years that certain flies may be bred from the dung of mammals. Réaumur (1740, plate 27) described the life history of *Scatophaga stercoraria* L. in cow dung, giving details of the egg, the larva, and the duration of development. He also described how the males await the females on the dung pat, and how the female deposits her eggs in the pat. The flies bred from cow dung may, as Rèaumur records for *Scatophaga*, use the dung or pat as a place of congregation for the sexes. Some flies, such as the small Sphaeroceridae (Borboridae), which as larvae feed on the dung, may also use the dung as food when adult and also shelter in or under the pat. Other flies, such as the Syrphid *Rhingia*, may frequent the dung as adults only for the purpose of oviposition, and others, such as females of the Muscid *Fannia* which do not oviposit in the dung, may use the dung as food. It is not surprising therefore that the older literature contains numerous references to the presence of characteristic species of flies on dung, and references to species bred from it (Degeer 1776, Bouché 1834, Kirby & Spence 1859, Westwood 1840).

Portchinsky (1885, 1910) was the first to describe as members of a complete ecological community the inhabitants of cow dung lying on the field. He described differences between those larvae which fed on dung and those larvae which were zoophagous and fed on coprophagous members of the community. He considered that the competition within the cow pat was keener than that between members of the carrion community which he also studied and that viviparous flies were more successful in a rapidly ageing habitat than were oviparous flies. Bogdanov (1901) treated the cow pat as a discrete community and described the seasonal succession and ageing succession of a pat, also discussing the effect of weather on the community. Experimental work was carried out in Java and Australia on the hornfly, *Lyperosia* (Handschin 1932, Krijgsman & Windred 1933), with reference to the reactions of adults and larvae to conditions in the pat.

Thomsen (1938) drew attention to the different fauna associated with piles of dung as manure, compared with the fauna of the more rapidly ageing pat lying on the field.

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Associated with Thomsen's work on the housefly was a very complete study by Hammer (1941) of the Muscidae and some other flies associated with cow pats in Denmark. A succession of species of ovipositing flies with ageing of the pat was described, and Hammer concludes that in cow pats the predacious beetle inhabitants particularly reduce the number of coprophagous flies, and that competition for food is hardly of any considerable importance. Hafez (1939) in Egypt had earlier recorded an ecological succession of insect visitors to fresh dung collected in experimental frames and a later succession of larvae living in the dung. Different kinds of dung were found to attract different species (Hafez 1947, 1948, 1949).

In America Mohr (1943) described the fly and beetle inhabitants of cattle droppings, and used the terms *micro-habitat* for the dropping and *micro-sere* for the succession of species found in the micro-habitat. An estimate, apparently by manual sorting, was also made of the numbers of larvae in the dung. Work similar to that of Hafez, Hammer and Mohr has not been published in Britain, and the fauna of cow dung has only been mentioned by a few authors, most of whom described the life-histories and early stages of some of the species (Thomson 1937, Goddard 1938, Coe 1942, Satchell 1947*a*, *b*; Kettle & Lawson 1952). Thus up to 1950 no published study was available describing the inhabitants living inside cow pats in terms of numbers and species, of seasonal change, of changes in numbers and species with ageing of the pat and of the possible action of the larvae inside the pat on one another. All the published estimates of competition or lack of competition inside the pat were derived mainly from adult counts and apparently unpublished results of larval collections.

THE LOCALITY INVESTIGATED AND THE BEHAVIOUR OF THE CATTLE

Rothamsted Experimental Station lies 25 miles north of London in the well-wooded countryside of Hertfordshire. The physical features of the district are described in the guide to the experimental farm (1947). Table 1 gives the grass minimum temperatures

Table 1. *Rothamsted: grass minimum temperatures 1950–51* (° *F.*)

	Mean	Highest	Lowest
Oct. 1950	37·9	49·9	18·7
Nov.	33·1	44·9	22·8
Dec.	27·5	39·7	17·7
Jan. 1951	30·6	39·8	18·5
Feb.	29·2	36·7	21·2
Mar.	30·8	46·7	20·6
Apr.	31·8	40·7	25·6
May	40·2	48·3	29·8
June	43·6	57·5	32·5
July	49·4	59·6	38·6
Aug.	48·3	56·7	38·9
Sept.	47·7	62·6	33·4

Temperatures reproduced by courtesy of Mr W. C. Game.

recorded by the Physics Department for the period 1950 to 1951, during which samples of the dung fauna were taken. Investigations into the fauna were restricted to five pasture fields at Rothamsted. These fields, Great Field, High Field, Parklands, Apple Tree and Baldwin's Paddock, lie in country that was once parkland of Rothamsted Manor (Fig. 1).

Different kinds of livestock at Rothamsted are usually separated in different fields when grazing. During the summer the cattle are usually kept in one field for about a month or two months and then moved on to another field (Fig. 2). In High Field, which is subdivided by wire fences, they may be moved from one part of the field to another and occupy this field for a longer period. Overwinter the practice appears to be to keep the older cattle in one field only and to feed these on hay, seed and roots.

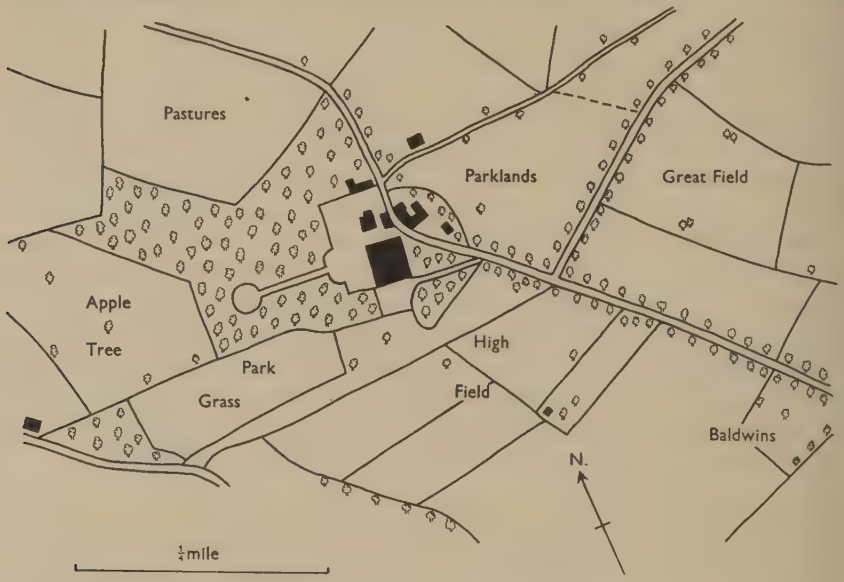

Fig. 1. Rothamsted Manor and the fields studied.

Such cattle are sold in the summer and are replaced by younger stock from the yard brought out to the fields in May. Consequently, one is unable to work in any one field right through the year, and also unable to work with any one herd. Longhorn bullocks were in the field from January to August 1950 and were replaced by Irish Shorthorn bullocks which overwintered and were joined by similar bullocks from the yard in May 1951. The behaviour of cattle has received only incidental study (Wardrop 1953). Overwinter they tend to keep close to the feeding trough during the day, but do wander and deposit their faeces elsewhere. At night they lie close together on the dryer part of the field. They may occupy the same part of the field for several nights and then suddenly move to a different part. Usually dung is deposited just after the bullock has got up and consequently the pats are often formed near one another and near the flattened depression made by the animal's body.

During the remainder of the year also the bullocks tend to keep together and all the animals will be grazing or lying down at about the same time. Although there is a tendency for cattle that have been resting to defaecate just afterwards (Thomson 1937), and as the cattle rest in groups the pats tend to lie together, this is by no means always true and faeces are deposited during grazing. Hammer (1941) gives the rate of deposition of faeces as seven to nine times a day, and Mohr (1943) gives it as ten droppings

a day. Wardrop (1953) gives averages of over ten defaecations a day. The pats studied were deposited by bullocks standing still, and these pats are almost circular.

The diameter of such pats varies from 5 to 18 in. (Mohr, 18–23 cm.).

Pats deposited by cattle that are moving are not deep and dry up too quickly for larvae to develop in them. Hammer (1941) mentions that dung deposited in the early morning is firmer than that deposited later in the day. It is not known how this affects the fauna. All the pats studied were deposited by bullocks in the period from early morning until mid-afternoon. It has not been possible to restrict this study to pats deposited at a more definite time of the day.

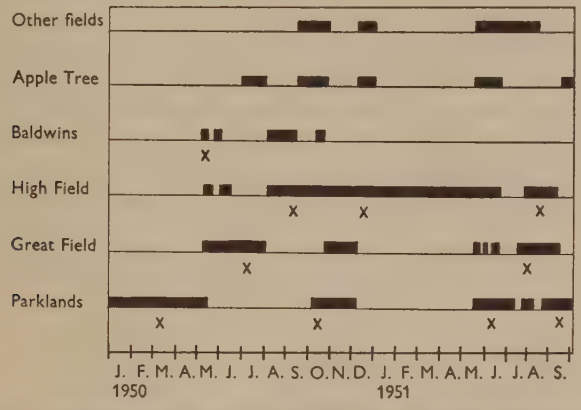

Fig. 2. Record of cattle movement between fields, 1950–51. X = field investigated at this time.

Hot dry weather during the summer affects the behaviour of cattle, for during the hot part of the day they shelter in the shade of trees in or around the field. Some of the flies visiting pats in the open field in spring and autumn tend to be restricted during the summer to shaded and more humid places, rarely occurring on pats in the open. The behaviour of the cattle provides a number of shaded pats in the summer and thus permits these species of flies to continue breeding in the dung.

THE FIELD DUNG DEPOSIT AS A HABITAT

When the cattle are feeding on grass in the summer the dung is quite liquid, but the surface soon dries and a crust is formed within a day. This crust apparently blocks the odour of the dung, for should the crust be broken at this time the dung will then attract adult flies (Hammer 1941). The colour of the dung also changes as it becomes older, from a darker to a lighter brown, although the rate of change depends on the position of the pat relative to shade and also on weather conditions. In hot weather in summer the dung is light brown with a thick crust at about 10 days old, but the last stage of the pat described by Mohr (1943) in America as 'light brown chip throughout' is rarely reached in this country and the old dung is always moist underneath. Dung deposited in winter is rather coarser in texture, as the cattle are then fed on hay and roots, and in winter the dung does not dry out on the surface to form a distinct crust. Handschin (1932) observed that the odour and the colour of the pats change

after the fourth day. Before this critical time the fresh dung will attract *Lyperosia* but not its parasite *Spalangia*. After this period *Lyperosia* is not attracted but *Spalangia* females are. Dung older than 10 days does not attract *Spalangia*. Krijgsman & Windred (1933) showed that *Lyperosia* is attracted to amines extracted from the dung. As the pat ages fairly rapidly and soon becomes unattractive to most adult flies for oviposition (Hammer 1941) the flies must be mobile and capable of following the herd about the field, and from field to field, to obtain fresh dung.

According to Handschin (1932), Hafez (1939) and Hammer (1941) the dung when deposited has a high water content of 73–89%. Hammer records that at the moment of deposition the pat has a temperature of about 37·5° C. (99·5° F.), the body temperature of a cow being 38–39° C. The temperature of the dropping falls by 5–7° C. within an hour at an air temperature of 18° C. (Hammer 1941, Fig. 6). The temperature of a dropping in the shade falls more rapidly than that of one in the open. When the dropping has cooled its temperature follows the temperature changes of the air above it. The temperature of the dropping near the ground is lower than, but follows rather closely, the temperature of the air at a height of 10 cm. during the day, while the surface of the dropping may be at a higher temperature (Hammer 1941, fig. 7).

Table 2. *Temperature relations (° C.) of pat to air temperature*

(From Hammer 1941, Table I.)

	Air, 10 cm.	Pat	
		Top	Bottom
Maximum			
Mean	24·02	23·64	19·23
Variance	16·48	21·62	7·13
Minimum			
Mean	10·92	13·34	14·52
Variance	7·67	4·49	2·43

At night the temperature at the bottom of the dropping is slightly higher than that of the surface or surrounding air. Consequently variation in temperature is less at the bottom of the dropping than at the surface or in the air just above the dropping (Table 2). Larsen & Thomsen (1940) have shown that temperature affects all stages of development in *Musca domestica* (egg, larval, pupal and pre-oviposition stages) and that temperature also affects the duration of egg, larval and pupal stages of the cow dung species *Lyperosia* and *Scatophaga*. As the rate of growth depends upon temperature, and as the larval stages can be determined satisfactorily only when they are mature, any attempt to estimate the changes in larval population during the year will be influenced by seasonal temperature changes (Table 3, Fig. 3).

The Dipterous larvae which inhabit cow dung are, when fully grown, generally amphipneustic (most larvae) or apneustic (Chironomidae and Ceratopogonidae). Exceptions are the larvae of *Scatopse* and *Dilophus* (peripneustic) and Tipulidae (metapneustic). Some of the amphipneustic may pass through the metapneustic stage in the early larval instars (Keilin 1944).

In the summer the crust formed on the surface of the pat separates from the more fluid dung underneath, leaving an air space beneath the crust. At this time of the year

the pat may be tunnelled by adult beetles (*Aphodius*, *Sphaeridium*, *Cercyon* and Trichopterygidae), and as these tunnels often remain open air is available to animals living in the centre of the pat. Growth of the vegetation beneath the pat may lift it from the ground. Dung deposited in the winter is not burrowed by beetles but may be invaded by earthworms (*Lumbricus castaneus* Savigny, det. J. Satchell) before the dipterous inhabitants have left. The winter dung is coarser owing to the inclusion of a large amount of straw, and is less fluid than dung deposited when the cattle are grazing. From the structure of the larvae inhabiting the dung in winter it appears that oxygen is as readily available at this time as it is in the summer. In fact, the winter larvae inhabiting the pat do not show the modifications of the posterior end, carrying the spiracles at the end of a siphon, shown by some summer larvae (*Psychoda*, *Rhingia* and *Sepsis*, Fig. 7). *Limosina crassimana* Haliday larvae are able to live in the stiffer winter dung and also in the more fluid dung of the summer.

As the dung ages the odour changes, and it is well known that, in the laboratory, horse dung may be inhabited by a succession of fungi (Massee & Salmon 1901–2). Although apparently a definite succession of fungi and bacteria in a cow pat has not been demonstrated in the field, it is tempting to suggest that the different species in the insect succession utilize different types of food available at different stages in the ageing succession of the pat, although moisture content of the dung may be most important (Krijgsman & Windred 1933).

THE LARVAL POPULATION

(*a*) *Seasonal succession*

It is possible to identify the families of all the larvae found in cow dung, and in certain families also the genus and species (Hennig 1948–52; van Emden 1942). Only fairly mature larvae can be determined with any confidence or without considerable labour, and all sampling of the pats for larvae has to be restricted to an age of pat when it is known that the pat contains mature larvae. As the rate of development of the larvae depends upon temperature, and as the temperature of the pat is determined by the time of year, the time that a pat is left on the field before sampling varies with the season. Fresh pats were marked on the day they were deposited with a white garden label carrying the date of deposition. Pats marked in this way could be found again fairly easily as the white label is conspicuous in the field. The time that a pat had to be left before most mature larvae appeared was determined by experiment in each month. The results are summarized in Table 3 and Fig. 3. The figures are adjusted for the months November to February, as in these months larvae are left for a period longer than 31 days and are affected by the temperature of the month following. The duration of development in these months is plotted against the two monthly mean temperatures. Pats were not marked during the rain.

Having marked the pat on the day of deposition, after a period of days depending on the time of year as expressed above, larvae were obtained from it by taking four 1 in. cores from each pat using a 1 in. diameter glass tube, which could easily be cleaned after use. It is relatively easy to take these cores of dung when the pat has not formed a hard crust on the surface. In the summer the crust had to be broken away to expose

the fluid dung beneath and an area of crust was taken which could only be approximately equal to the area of the tube. However the crust contains few larvae, and most of these occur in the thin film of wet dung adhering beneath the crust surface, so the error in slightly altering the method of sampling may be presumed to be small.

Table 3. *Temperature and age of pat before sampling for larvae*

	Mean age of pat before sampling (days)	Range (days)	Mean grass minimum temperature (° F.)
Oct. 1950	13	7–21	37·9
Nov.	38	15–68	30·3*
Dec.	48	43–57	29·1*
Jan. 1951	34	31–38	29·9*
Feb.	35	29–41	30·0*
Mar.	25	21–30	30·8
Apr.	18	15–21	31·8
May	15	9–19	40·2
June	8	6–15	43·6
July	6	4–8	49·4
Aug.	7	6–8	48·3
Sept.	8	7–9	47·7

* Corrected two-monthly means.

Each core was carried back to the laboratory in a separate jar, and the larvae then were washed out of the dung by using a 25% solution of magnesium sulphate (Ladell 1936). By stirring until no more larvae floated to the surface an accurate estimate of the numbers of larvae per core could be made by picking the larvae off the surface of the solution and sorting and counting them in a separate dish of water. After washing

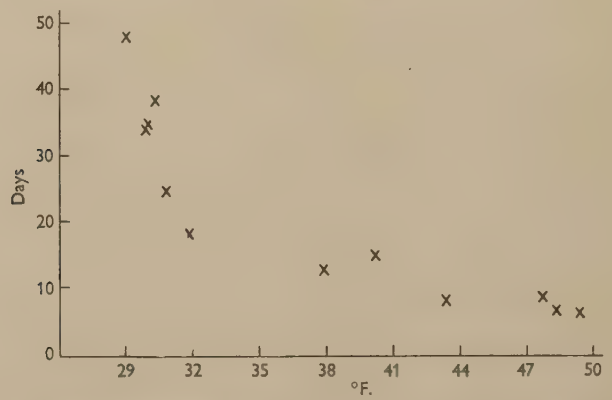

Fig. 3. The relation between the monthly mean grass minimum temperature and the monthly mean period for which the pats were left after deposition before sampling for larvae.

in water the larvae could be placed in dung to continue development or could be preserved in alcohol. Using this method it was possible to sample about ten pats in each month and the sampling was carried out from October 1950 until September 1951 (Table 4).

Since no two pats are deposited at exactly the same time or in exactly the same place, one may expect considerable differences between populations in different pats. Despite these expected differences a well-marked seasonal succession of larvae has been observed and an estimate has been made of the numbers of larvae in each month. This estimate has been restricted to pats which were not shaded for any great length of time and also ignores the larvae which occur later in the ageing succession of the pat in the summer.

Table 4. *Number of pats containing full-grown primary larvae sampled per month*

	Pats		Pats
Oct. 1950	8	Apr. 1951	17
Nov.	22	May	10
Dec.	8	June	14
Jan. 1951	16	July	9
Feb.	22	Aug.	11
Mar.	14	Sept.	10
		Total pats	161

The seasonal succession of animals in the pat can be expressed as the percentage of pats occupied in each month of the year (Table 5, Fig. 4). 'Month' here refers to the month in which the pat was deposited and the eggs laid. The larvae developing in these pats may in the winter be full grown in the following month. The number of pats investigated in each month is small but it is believed that the percentage of pats occupied does reflect the seasonal occurrence of the various animals. To take one example only, Hammer (1941) records that adults of *Scatophaga stercoraria* L. have two peaks of abundance in the open field, one from April to May, and one from September to November, and the adults disappear from the open field from June until August. The same seasonal occurrence of adults has been found at Rothamsted, the flies becoming more abundant in the shade (of woods and the park drive) in June and July and less abundant in the open field. This change in abundance of adult *Scatophaga*, the males of which are very conspicuous on the dung, is reflected in a similar change in percentage of pats inhabited by *Scatophaga* larvae (Fig. 4), and also in the geometric mean number of larvae recorded per month (Fig. 5). The method of sampling was also sensitive enough to record single first-instar *Scatophaga* larvae (readily identifiable by the saw-like mandibles and posterior tubercles) in the dung in January and February. *Scatophaga* adults are rare at this time of year (Table 15). Mellor (1919) and Hammer (1941) record hibernation in the pupal stages, although Cotterell (1920) records that adults hibernate. This latter opinion is supported by the finding of a single young larva in dung deposited in January and February indicating the presence of ovipositing females in the field. The percentage of pats inhabited as estimated also coincided with the abundance of adults of other species visiting dung.

All the pats investigated contained larvae of some kind. The lowest count was a pat deposited on 14 February 1951. Three cores of dung contained no larvae, one core contained one larva of *Copromyza nitida* Mg. Two pats deposited on the same day, but not at the same time or in the same position, contained respectively fifteen *C. nitida* larvae, and four *C. nitida* larvae, one undetermined larva and one earthworm. It appears that the undisturbed pat is at no period of the year completely uninhabited.

There are marked changes in the abundance of each animal. Few genera are present throughout the year. The genus *Limosina*, containing several species, is exceptional in that it is fairly widely distributed over the field in all months of the year. As might be expected several genera are absent in the winter. Larvae of the Muscidae and Sepsidae are absent in the coldest months from December until April and the species enter into a diapause over these months (Hammer 1941). Rather surprisingly, other genera occur mainly in the winter and disappear from the field as the temperature increases. Larvae of *Trichocera* and *Smittia* enter a diapause over the period when the temperature is high. Larvae of *Trichocera* collected in the winter do not emerge until the following October or later. Larvae of *Smittia contingens* Walk. and *aterrimus* Mg. collected in April did not emerge in the laboratory until August and September. The winter Sphaeroceridae, however, emerge in the early summer, but the summer

Table 5. *Percentage pats inhabited by larvae*

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
Limosina	62·5	91·0	62·5	31·0	73·0	100·0	94·0	80·0	86·0	100·0	100·0	100·0
Copromyza	0	59·0	100·0	87·5	100·0	78·5	88·0	30·0	0	11·1	9·1	50·0
Sepsidae	0	0	0	0	0	0	5·9	100·0	100·0	100·0	100·0	70·0
Psychoda	100·0	82·0	12·5	12·5	0	21·5	82·0	100·0	71·5	44·5	54·5	30·0
Trichocera	25·0	86·0	87·5	69·0	18·2	0	0	0	0	0	0	0
Scatophaga	75·0	69·6	0	6·3	4·5	14·3	47·0	50·0	7·0	0	0	30·0
Predacious Muscidae	62·5	13·8	0	0	0	0	0	0	71·5	100·0	100·0	80·0
Hydrophilid larvae	0	4·6	25·0	12·5	0	14·3	47·0	50·0	86·0	78·0	45·5	0
Muscidae	75·0	22·5	0	0	0	0	0	40·0	21·5	50·0	55·0	50·0
Smittia	12·5	32·0	50·0	25·0	13·6	21·5	17·6	0	0	0	0	0
Scatopse	0	0	0	6·3	0	0	0	0	28·5	40·0	73·0	10·0
Staphylinid adults	12·5	0	25·0	12·5	9·1	57·0	88·0	30·0	43·0	60·0	55·0	40·0
Collembola	12·5	27·5	75·0	75·0	50·0	43·0	17·6	0	14·3	0	9·1	50·0
Oligochaeta	0	32·0	62·5	31·3	41·0	36·0	23·6	0	0	0	0	0
No. of pats	8	22	8	16	22	14	17	10	14	9	11	10

No pats were in complete shade.

generation apparently occupies another habitat at this time of the year and does not live in the pat in the open. The adults of those flies that have a maximum abundance of larvae in the cow pat in winter, *Trichocera*, *Copromyza nitida*, *Limosina crassimana* Haliday, *L. silvatica* Mg., and *Smittia*, must be capable of flying or walking at surprisingly low temperatures.

There is another group which occurs abundantly in the spring, becomes less numerous in the summer, and reappears in abundance in the autumn. The distribution of *Scatophaga* has been mentioned previously, and Hammer (1941) records a similar distribution for the Muscid *Haematobia stimulans* Mg. In both these species the bimodal distribution is not due to the presence of two separate generations as the duration of development is only 20–30 days in the summer. At Rothamsted *Psychoda phalaenoides* L., *Copromyza hirtipes* Rob.-Des. and *Limosina scutellaris* Haliday have a rapid development, and these also occur in the field in spring and autumn, and disappear in the summer. Hammer (1941) supposes the summer decline of *Scatophaga* and *Haematobia* to be due to the sensitivity of larvae and adults to the higher temperatures which may be fatal. However, the decline in numbers may be more apparent than real. The estimates were made of populations in the open, and instead of greater

mortality in the summer the decline may be accounted for by a change in habitat of the adults as the temperature increases and the humidity decreases. Although larvae of *Scatophaga*, *Copromyza* and *Psychoda* have rarely been found in the summer in pats in the open they have been found in abundance in pats in almost continuous shade. As the cows shelter in these shaded places a number of shaded pats are provided which permit the flies to continue their reproduction during the summer away from the higher temperatures of the open field, although the shaded pats, being distributed over

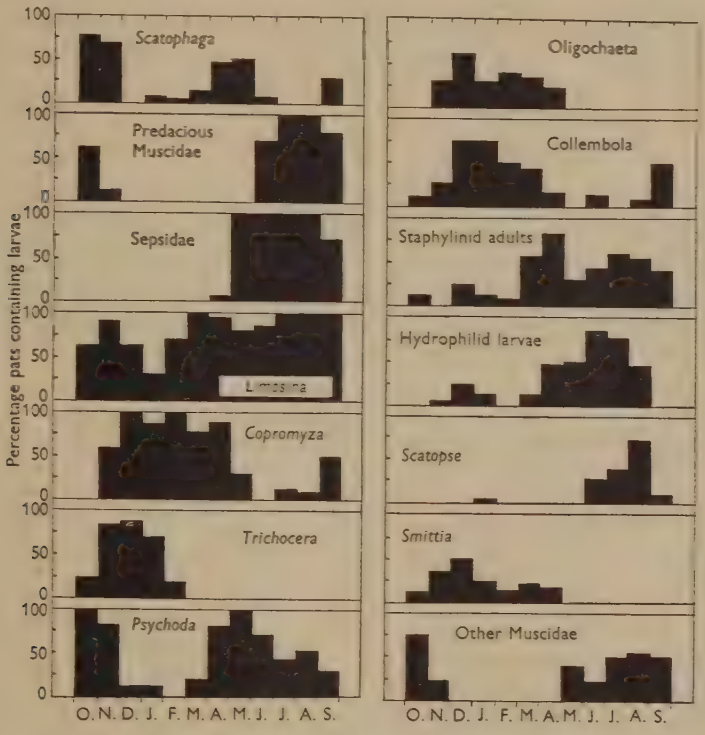

Fig. 4. Seasonal succession of larvae in cow pats. Recorded as percentage of pats containing larvae.

a small and well-used area, are liable to be trampled on by the cows. It is interesting that the Ichneumonid and Braconid parasites visiting pats in the summer are almost always found on shaded pats.

The presence of marked differences in the seasonal abundance between species and genera in cow pats shows that there is not one coprophagous community, but a series of coprophagous communities, depending upon the season of the year, which replace one another during the year.

(*b*) *Numbers of larvae*

Where the number of animals recovered is sufficiently great the seasonal succession can be expressed as the arithmetic mean number of larvae per 4 × 1 in. cores per month and the standard error of each monthly mean can be worked out. The mean

number of larvae per 4 × 1 in. cores can be converted into approximate number of larvae per pat. The number of 1 in. cores that can be taken from a pat of 6 in. diameter is approximately thirty; therefore multiply figures for four cores by eight to give mean number per pat. The standard error of the monthly means is large, amounting on the average to about 25% of the mean. However, each pat investigated differed in place and time of deposition and consequently in the numbers of eggs laid on it by ovipositing females (Table 6). Hammer (1941) has shown that the numbers of adult Muscidae

Table 6. *Number of* Psychoda *larvae in cores of dung in three pats deposited 8 November 1950*

Core ...	1	2	3	4
Pat 1, sampled 28 Nov.	47	28	44	17
Pat 2, sampled 29 Nov.	207	132	377	180
Pat 3, sampled 30 Nov.	1	9	0	20

and *Scatophaga* vary during the day. In the present study grouped within each month are the numbers of larvae recorded from pats deposited on different days. Weather conditions vary from day to day. Despite the factors causing variation in numbers of larvae between pats it is possible to show that the numbers of larvae belonging to different genera reach maximum abundance at different times of the year (Table 7). Again one has a picture not of one static coprophagous community but of a community changing during the year with the season.

Table 7. *Arithmetic mean number of larvae per 4 × 1 in. cores per month and standard error*

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
Limosina	5·5	6·3	4·47	2·5	11·2	52·6	27·0	9·0	9·8	32·1	33·9	6·2
S.E.	3·37	1·82	1·83	1·6	2·5	14·9	14·4	2·4	3·06	9·3	7·8	1·5
Copromyza	—	9·3	12·9	19·9	22·8	4·7	16·2	2·8	—	—	—	1·7
S.E.	—	2·7	2·4	5·96	3·7	1·4	5·8	1·6	—	—	—	0·74
Sepsidae	—	—	—	—	—	—	0·9	21·8	69·0	55·7	42·3	3·7
S.E.	—	—	—	—	—	—	0·86	3·02	11·1	11·19	8·36	1·5
Psychoda	532·4	87·0	—	0·25	—	0·29	59·0	96·2	3·8	1·44	3·45	0·5
S.E.	197·0	41·0	—	0·18	—	0·16	26·2	52·5	1·35	0·7	1·6	0·27
Trichocera	2·0	9·8	37·1	7·5	0·3	—	—	—	—	—	—	—
S.E.	1·4	2·42	8·9	2·5	0·13	—	—	—	—	—	—	—

To convert to approximate average number of larvae per pat multiply by 8.

The numbers of other larvae have been recorded in each month but the numbers collected are too small and too variable for any demonstration of significant changes in numbers between months. The seasonal appearance of these larvae has been given in Fig. 4 and in Table 5. The arithmetic mean number of individuals per inhabited pat sample over all months and the standard error of this mean has been worked out for these larvae (Table 8).

The numbers of larvae per month can also be expressed as the geometric mean number of larvae per pat sample (4 × 1 in. cores). This mean is less affected by extreme values than is the arithmetic mean (Williams 1937). The geometric mean number of larvae per month has been worked out (as $\frac{\Sigma \log n+1}{x}$, see Williams 1937) for the six

most abundant types of larvae (Table 9, Fig. 5). The seasonal distribution recorded in this way follows the type of distribution already described from percentage distribution over the field and from the arithmetic mean values.

Table 8. *Arithmetic mean number of larvae per occupied pat for all months*

	Number of pats inhabited	Mean number per inhabited pat sample	S.E. of mean
Scatophaga	48	13·8	2·9
Predacious Muscidae	47	3·6	0·4
Other Muscidae	34	3·5	0·6
Smittia	25	3·6	0·7
Scatopse	18	4·5	1·5
Hydrophilid larvae	44	2·9	0·4

To convert to approximate number per pat multiply by 8.

The total numbers of larvae and other animals recorded by taking fairly regular samples of cow pats for a year at Rothamsted between October 1950 until September 1951 are given in Table 10. These numbers are the numbers present at the age of the pat in the open field when most Dipterous larvae were mature. Comparing the numbers found the most abundant animals, at this age of pat, are those whose seasonal occurrence has already been described. More *Psychoda* larvae have been found than have larvae

Table 9. *Geometric mean number of larvae* $= \text{anti-log}\dfrac{\Sigma \log n + 1}{x} - 1$

	Limosina	*Copromyza*	*Trichocera*	Sepsidae	*Psychoda*	*Scatophaga*
Oct.	2·7	—	0·7	—	**330·8**	2·2
Nov.	4·3	3·2	3·8	—	17·4	**4·4**
Dec.	2·4	11·0	**19·9**	—	0·09	—
Jan.	0·7	10·5	3·1	—	0·12	0·04
Feb.	3·8	**14·8**	0·2	—	—	0·04
Mar.	**34·4**	2·5	—	—	0·2	0·2
Apr.	15·8	5·9	—	0·2	13·1	1·7
May	5·3	0·7	—	17·3	**22·6**	**2·1**
June	5·6	—	—	55·0	3·0	0·2
July	15·9	—	—	**59·1**	0·8	—
Aug.	**23·3**	—	—	33·5	1·6	—
Sept.	5·3	1·0	—	1·8	0·3	1·4

To convert to approximate number per pat multiply by 8.

of any other genus. These larvae occur in pats in the open during a limited part of the year and consequently at the time of occurrence are extraordinarily abundant. Up to 598 larvae have been recorded from a 1 in. core of dung (Table 11), and in May and October when the larvae are mature the whole surface of the pat may be moving. Larvae of *Limosina* occur during the whole of the year, and consequently the numbers of these larvae at any time are not so great. The Sepsidae occur over a more restricted period of the year and are very abundant in the dung at this time. The larvae of *Copromyza*, *Scatophaga* and *Trichocera* are larger and not so numerous, although by weight they may consume more of the pat than the more abundant smaller larvae. The maximum number of *Psychoda* larvae recorded accounted for one-tenth of the weight of the dung core (10 g.). The maximum number of *Scatophaga* larvae recorded

in a 1 in. core was 53. The weight of these larvae was approximately 1·7 g. (Larsen & Thomsen 1940). The weight of the core from which they were recovered was 11 g. so that the bulk larvae of *Scatophaga* may at times exceed the more numerous *Psychoda* larvae.

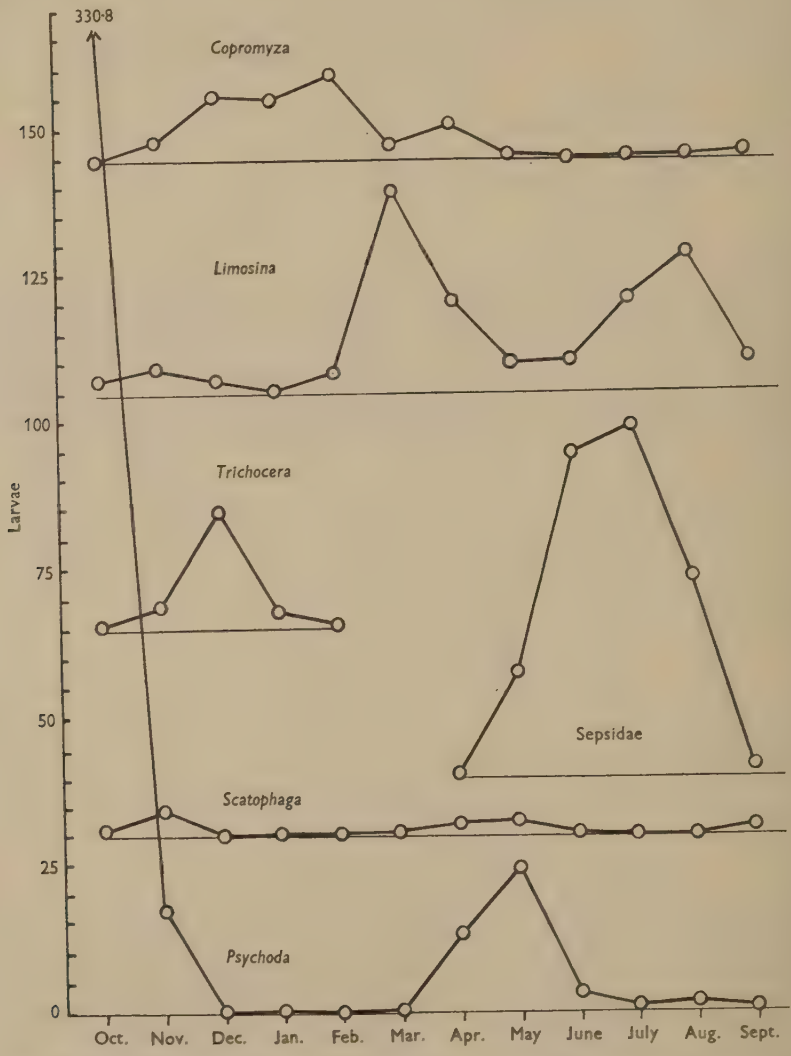

Fig. 5. Seasonal succession of larvae in cow pats. Numbers of larvae recorded as geometric mean number of larvae per pat sample of four 1 in. cores for each month.

The 18,860 individuals were recovered from 161 pats or 644 1 in. cores. On an average there are 29 individuals per 1 in. diameter core of cow dung. Supposing the diameter of the pat to be about 6 in., which is too low for most, then the surface is

large enough to take say thirty 1 in. cores from it. Therefore, on an average, each pat contains 29 × 30 individuals or approximately 1000 inhabitants. The number of pats produced each day has been estimated as 7 to 10. All these may not be suitable for

Table 10. *Total numbers of animals obtained from cow pats at Rothamsted, October 1950–September 1951*

Psychoda	8269	Syrphidae	3
Limosina	2755	*Sciara*	1
Sepsidae	2267	Collembola	415*
Copromyza	1513	Staphylinid adults	278
Scatophaga	660	Staphylinid larvae	110
Trichocera	649	Hydrophilid adults	32
Predacious Muscidae	168	Hydrophilid larvae	125
Other Muscidae	118	*Aphodius* adults	16
Smittia	89	*Aphodius* larvae and eggs	41
Scatopse	81	Trichopterygid adults	3
Anisopus	560	*Onthophagus*	1
Culicoides	357	Figitid adults	2
Stratiomyidae	109	Diplopoda	1
Empididae	45	Acarina	16
Cecidomyidae	5	Oligochaeta	171

Grand total = 18,860

* Figure too low as some specimens escape by jumping from the surface of the washing solution. Nematodes and smaller organisms not recorded.

habitation. Often the dung is trodden on by the cows, or the cow may move while defaecating, or the pat may be disturbed by birds. Also all will not be deposited away from shade or during the day, and the numbers of larvae recorded are only from pats in the open deposited during the day. However, if we take the number of pats per day as six, which is too low, then the cow produces 6 × 365 pats a year, or supports

Table 11. *Maximum number of larvae per 1 in. core of dung*

Psychoda	17 Oct.	598
Limosina	1 Apr.	230
Sepsidae	18 June	76
Copromyza	27 Jan.	56
Trichocera	5 Dec.	37
Scatophaga	1 Nov.	53
Predacious Muscidae	17 Oct., 30 July	7
Hydrophilidae	15 June	7
Scatopse	13 June	10
Anisopus	23 July	29
Culicoides	19 May	58
Polietes	17 Oct.	7
Dasyphora	7 May	14
Mesembrina	several	1
Empididae	19 Sept.	9
Stratiomyidae	18 June	19
Smittia	14 Nov.	15
Staphylinidae	10 July	37

1000 × 2190 inhabitants of cow dung per year or approxi mately 2,000,000 inhabitants mostly dipterous larvae.

The probable weight of larvae produced in a year can be estimated roughly. It is known that 500–600 *Psychoda*, or 30 *Scatophaga*, or 25 larger Muscid larvae weigh

approximately 1 g. One can grade the other larvae according to size and estimate in this way very roughly their living weights:

Group I	*Psychoda*, *Limosina*, Sepsidae	Approx. 500 individuals per gram.
Group II	*Copromyza*, *Trichocera*	Approx. 100 individuals per gram.
Group III	*Scatophaga*	Approx. 30 individuals per gram.
Group IV	Coprophagous Muscidae	Approx. 25 individuals per gram.

The total weight of 18,860 individuals must therefore be about 80 g. This is the approximate weight of living animal material in 644 1 in. cores of dung. The weights of the 1 in. cores varied from 3 g. in May to 26 g. in February, but the weights are distributed around a mean of 10 g., weighing slightly less in summer and rather more in winter. The weight of the 644 cores may be approximated as 6440 g. Of this 80 g. at least is living animal, or one-eightieth of the pat by weight is living animal material. Henry & Morrison (1923) have shown that a bullock may produce 52 lb. of dung a day for every 1000 lb. of live weight. During a year therefore a bullock produces $52 \times 365 \times 10^{-3}$ or nineteen times its own weight of dung. Of this one-eightieth would later be animal matter utilizing the dung as food. It appears that an apparently efficient animal such as a cow leaves in its faeces enough food material in a year to support an insect population, mostly dipterous larvae, equal to at least one fifth of its own weight.

(*c*) *Ageing succession in the pat*

The previous figures are possibly minimum values as they are derived from only one stage in the succession of larvae in the cow pat with age, and do not include all the inhabitants of cow dung. Surprisingly few muscid larvae were found compared with larvae of other families. In the summer coprophagous muscid larvae mature in 5 days and later leave the pat to pupate. According to Thomson (1937) some larvae arrive at the third instar within 3 days at a temperature of 18° C. Four pats in July were sampled on the fourth day after deposition, but these did not contain more muscid larvae than pats sampled on the sixth and eighth days. Also coprophagous muscid larvae were found in all months from May until November. It is possible, however, that the rapidly maturing larvae of *Cryptolucilia* and *Dasyphora* were missed. If the dung is sampled earlier in the summer then the larvae of the Sepsidae and Sphaeroceridae would be too young to determine easily. For the same reason the numbers of Lamellicorn beetle adults which feed on the fresh pat (notably the species of *Aphodius*) have not been estimated, as most of these beetles have left by the second day. Some of the Staphylinid adults also have been noticed only on fresh dung, but some of these are predators. Mature *Aphodius* larvae were conspicuously absent from the dung cores taken, and have been found only in rather dry cow pats over 20 days old in summer. Large eggs were found in the cores of dung taken in April and June and these developed into *Aphodius* larvae. Thirty-three of these eggs have been recovered from the dung samples and only eight small larvae. Obviously the cow pat

was being sampled too early for *Aphodius*. Mohr (1943) is also of the opinion that despite the presence of adult lamellicorns in the fresh dung the larvae belong to the later stages of the succession. He also points out that although several species of adult *Aphodius* visit dung, only larvae of a few species develop in the pat.

Included in the Table 10 are some genera and families of dipterous larvae which have not been mentioned in the section on seasonal changes in the population of larvae. Although these larvae may occur in more than one month they are of infrequent occurrence and some of them, Stratiomyidae, *Anisopus*, *Culicoides*, are immature when the pat is sampled for the larvae of Sphaeroceridae, Sepsidae, etc. The sporadic manner in which the immature larvae occur is shown by considering Table 12. Of the *Culicoides* larvae collected in June, forty-nine of the sixty-four occurred in one pat

Table 12. *Secondary larvae recorded by routine sampling*

	Stratiomyidae	Empididae	*Anisopus*	*Culicoides*
Jan.	—	4	—	—
Feb.	—	1	—	—
Mar.	—	1	—	—
Apr.	—	2	4	—
May	—	—	134	198
June	98	6	36	64
July	1	—	37	—
Aug.	—	7	107	2
Sept.	4	19	211	—
Oct.	6	5	31	93

sampled at 6 days but not washed until 15 days old. Of the 198 larvae recorded in May, 134 occurred in one pat 16 days old. All the *Culicoides* larvae found in the normal sampling were immature. Young larvae of *Anisopus* were also recorded sporadically. All the thirty-six larvae recorded in June were from two pats only (15 and 8 days old). The larvae recovered in July and August were also very young and no *Anisopus* larvae in any month were approaching full size. All the stratiomyid larvae were immature, and it is known that a number of stratiomyid species have a long larval period (Smith 1920, Buxton 1936, Hammer 1941). Of the empid larvae twelve came from one pat in September.

Of three pats deposited on 7 June 1951 two were sampled for larvae as usual after 10 days. Eggs and small larvae of *Aphodius* were present, as well as the expected larvae of Sepsidae, *Limosina*, *Psychoda* and Muscidae. In one pat also were present some immature *Culicoides* larvae. The other pat was left for 21 days and then sampled for larvae. Large and small *Aphodius* were present and also mature *Culicoides*. Larvae of *Limosina* were present but these differed from the larvae previously recognized in the fresh dung in having short anterior spiracles. *Limosina collini* Richards adults were bred from these larvae, whereas *L. lugubris* Haliday and *L. scutellaris* Haliday were normally bred from larvae in fresh dung. Puparia of *Sepsis* were also present, and all these had long posterior siphons resembling *S. flavimana* Mg. (Fig. 6). It had been previously recognized that in normal sampling for larvae two age-groups of sepsid larvae could be expected. One group consisted of mature larvae with short posterior siphons (Fig. 6) and these larvae developed into *S. cynipsea* L. and *Pandora scutellaris* Fall. (Table 13). The other group of larvae was not so mature, although a

few larvae might be in the last instar. This group consisted mostly of larvae with long posterior siphons (Fig. 6) and such larvae develop into *Sepsis flavimana* Mg. and *S. pilipes* v. d. Wulp. That there are two groups of sepsid larvae developing at different rates is shown by breeding adults from dung (Fig. 7). In older pats the second group of sepsid larvae becomes mature, and consequently puparia of this group were found in the older pat.

Fig. 6. Lateral views of posterior ends of larvae of (*a*) *Sepsis flavimana* (*b*) *S. cynipsea* to show differences in length of siphon.

The different associations of primary and secondary flies (in the sense of Fuller 1934) is shown by examination of overwintering dung from the previous year examined in the spring of the following year. Larvae found in the dung at this time are hibernating, and in March 1950 two associations of larvae were found in cow pats of unknown date of deposition in Apple Tree Field. From knowledge of the seasonal succession it is

Table 13. *Sepsidae (adults) bred from larvae obtained by routine sampling, June and July 1951*

		Condition at time of sampling	
		Mature	Immature
Sepsis cynipsea L.	Males	32	—
S. flavimana Mg.	Males	1	6
S. orthocnemis Frey	Males	—	6
S. pilipes v. d. Wulp	Males	—	3
S. nigripes Mg.	Males	—	3
S. fulgens Mg.	Males	—	1
Sepsis	Females	47	40
Pandora scutellaris Fall.	Males and females	8	2
	Total	88	61

suggested that the group (Table 14) containing *Trichocera*, *Scatophaga*, *Copromyza nitida* Mg. and *Limosina silvatica* Mg. was obtained from pats deposited when the cows were in the field in November. Before this date the cows were present in the field in September (?) and this would account for the presence of *Sepsis pilipes* v. d. Wulp, *Limosina collini* Richards and *L. pseudoleucoptera* Duda, and other species associated in pats 9–14 (Table 14). *Culicoides*, *Sepsis pilipes* and *Limosina collini* are believed to be secondary flies and so are the other flies associated with them. Larvae of the midges *Camptocladius* and *Forcipomyia* were not found during the routine sampling. However, *Forcipomyia* larvae are known to occur in old dung, in July in 17- and 21-day-old pats, and *Camptocladius* has been found visiting and also has been bred from the older dung in the summer (see also Strenzke 1950). Mature *Forcipomyia* larvae have been found in old dung associated with mature *Anisopus*

and maturing *Aphodius* larvae. As mentioned previously, it is tempting to suggest that the different stages of the ageing succession feed on different types of food, the late stages feeding primarily on moulds. Five species of *Sciara* were bred from dung but only from old pats, and *Sciara* larvae are known to be fungus feeders (Baumberger 1919).

Table 14. *Overwintering associations of primary and secondary flies, January to March 1950*

	Pat numbers													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Trichocera	+	+	+	+	+	+	+	+	.	.	.	.	.	.
Smittia	.	.	.	.	+	+	.	.	+	.	.	.	.	.
Scatophaga	+	.	+	.	.	.	.	.	.	.	.	.	.	.
Copromyza	+	+	+	+	+	.	.	+	.	.	.	.	.	.
Limosina	+	+	+	+	+	+	+	+	+	.	+	.	.	+
Sepsis puparia	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Forcipomyia	.	.	.	.	.	.	.	.	.	+	.	.	+	+
Culicoides	.	.	.	.	.	.	.	.	+	.	.	.	+	.
Camptocladius	.	.	.	.	.	.	.	.	+	+	+	+	+	+
Empididae	.	.	.	.	.	.	+	+	+	+	.	+	+	+

(*d*) *Larval populations in shaded pats*

All the estimates of numbers of larvae so far discussed were obtained from samples of dung taken from pats lying in the open field and not shaded for long periods. Dung dropped in parts of the field shaded by trees in contrast to dung in the open rarely forms a distinct thick crust, and often is covered by small red fungi (*Humaria* ?). The few observations available, mostly from five pats sampled in June and July, show that larval populations of the shaded pats in summer may be different from the populations already described of pats in the open.

Thomson (1937) records *Morellia* larvae as commonest in pats in the shade, and Hammer (1941) records that *Polietes* adults are reluctant to appear in the sunshine but soon appear on a shaded pat. He also records similar adult habits in *Mesembrina*, *Mydaea* and *Azelia* in the Muscidae. At Rothamsted in the summer *Morellia*, *Polietes* and *Azelia* adults have been found frequently on dung beneath trees but are rare in the open. *Polietes* adults are extremely common in the shade in June but larvae of *Polietes* did not appear in the open field until the cool of the autumn (September to November). Hammer (1941) also says that *Scatophaga* adults are reluctant to appear in the open field at the height of the summer, although they are seen in the sunshine in early and late summer. Other flies in Britain appear to behave similarly, and larvae of these species can be found in shaded pats in the summer. At Rothamsted in late June pats in the shade have been noticed with the surface covered with larvae of *Psychoda phalaenoides*, a condition similar to that found in the open in May and October. Larvae of *Scatophaga*, *Morellia*, *Copromyza hirtipes*, *Limosina scutellaris* and *Psychoda phalaenoides* have been found commonly in shaded pats in summer (June-August) but not, or very rarely, in pats in the open. Records of *Scatophaga* from light traps at Rothamsted show that by collecting *Scatophaga* at night, when the humidity is high, this species can be shown to be frequent in the

summer months (Table 15). Presumably in the heat of the summer this species may continue to reproduce in the more humid parts of the field, in shade, or in woodland.

Table 15. *Light trap recordings of* Scatophaga, *1933–35 and 1948–49*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Total number recorded	4	3	2	261	155	699	371	521	1008	1009	648	71

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DURATION OF DEVELOPMENT

The duration of development of the flies has been taken to be the period from the day of deposition of the pat to the day of emergence of the fly. This neglects the length of life of the adult fly. Larsen & Thomsen (1940) have shown that *Scatophaga* at 20° C. has a pre-ovipositional period of about 14 days. It also neglects the possibility that adult females may lay eggs on dung more than 1 day old. The parthenogenetic *Psychoda severini* Tonnoir can continue for several generations on dung kept moist in a jar, and this species is regarded as a secondary fly. It seems very likely that the inhabitants of the older dung such as *Sciara* and *Psychoda albipennis* Tonnoir will

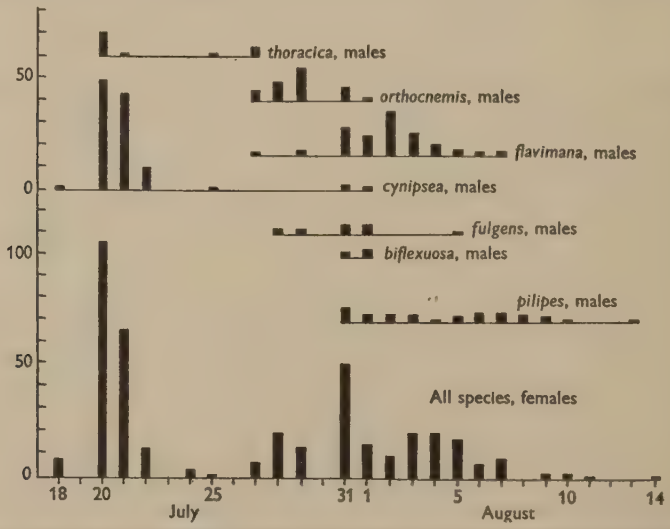

Fig. 7. Emergence succession of species of *Sepsis* from dung deposited on 5 July 1950. Ordinate scale in tens of individuals.

breed in any type of moist humus. *Camptocladius* adults have been found associated only with 7–15-day-old pats, and *Limosina collini* Richards adults are commonest on dung about 10 days old, in contrast to adults of *L. lugubris* Haliday and *L. scutellaris* Haliday which oviposit in fresh dung. However, in the absence of more detailed knowledge the duration of development has been taken as though all the eggs are laid when the dung is fresh. Most species of Diptera living as larvae in the cow pat in the summer have a period of development of under 40 days. Different species in the same genus, of *Psychoda* (Satchell 1947*b*), *Sepsis* (Fig. 7) and *Limosina* (Table 16), may have

different periods of development. In these genera the species regarded as primary from the larval sampling, those which develop first in the cow pat, emerge earlier than those species regarded as secondary. In the Nematocera, *Anisopus*, *Culicoides* and *Scatopse*, the larvae mature slowly and consequently occur late in the pat. The pupational period is short in *Anisopus* and *Culicoides*, as it is also in *Psychoda* and *Trichocera*, so that the total duration of development may be no greater than that recorded for some of the Muscidae, the larvae of which mature very quickly but which have a long pupational period (Thomson 1937). A few species such as the stratiomyids *Sargus* and *Microchrysa*, and the midge *Camptocladius* have a much longer period of development, 60–100 or more days, and in the case of the Stratiomyidae the pat may disintegrate before development is completed. Hammer (1941) records a larva of *Sargus* surviving into the second year after deposition of the pat and a *Sargus* larva at Rothamsted was still alive in the summer of 1953 in a tube of dried dung first deposited on 16 September 1951.

Table 16. *Numbers of* Limosina *species which emerged from a cow pat deposited 5 July 1950*

	Days after deposition of the pat						
	18–22	23–27	28–32	33–37	38–42	43–47	48–52
lugubris Haliday	445	366	216	22	—	—	—
crassimana Haliday	25	5	—	—	—	—	—
scutellaris Haliday	1	24	22	15	5	4	2
collini Richards	—	—	3	9	5	2	1
pseudoleucoptera Duda	—	—	—	1	—	1	—
denticulata Duda	—	—	4	9	9	3	—
aterrima Haliday	—	—	1	1	—	—	—

In winter the sphaerocerid larvae in a pat develop much more quickly if the temperature is raised. Most take 90–200 days before emergence at normal temperatures. This is not so with the larvae of *Trichocera*, and the midge *Smittia* which have a diapause as the temperature increases. In these latter species the pat probably disintegrates before development is completed.

PREDACIOUS AND PARASITIC ORGANISMS

The hydrophilid and predacious muscid larvae live in the pat and prey upon other coprophagous larvae (Portschinsky 1885, 1910; Keilin 1917; Thomson 1937; Hammer 1941). These predacious larvae are widely distributed over the field (Fig. 4) and occur mainly from April until September (Table 17). Between April and October 10,978 coprophagous larvae were obtained (Table 17), and these were associated with 282 predacious larvae. The primary coprophagous larvae mature more quickly than the predacious larvae which may be found still active in fairly old dung. Hammer (1941) records that *Sphaeridium*, in the Hydrophilidae, fed on 32–36 sepsid larvae before ceasing to feed, and suggests that if ten *Sphaeridium* larvae survive in each pat these will have killed at least 250 *Cryptolucilia* larvae. Thomson (1937) records single larvae of the muscid *Hebecnema* feeding on 16–20 *Cryptolucilia* and single larvae of *Mesembrina* feeding on 10–46 *Cryptolucilia*. Two specimens of *Mesembrina* in the British Museum collection are recorded as bred from larvae that devoured 30–40 *Musca autumnalis* Deg. larvae. Prey are not so readily available in the pat as they are by

feeding in culture, and *Mesembrina* larvae can mature on pure dung. Also the predacious larvae will attack one another. Supposing, however, that each predacious larva is capable of eating twenty coprophagous larvae at the stage at which they were collected, then the predacious larvae will reduce the population of coprophages by $(282 \times 20) \div 10{,}978$ or by 51%. This presumes that the predacious larvae are still actively feeding, that no selective feeding takes place, and that the larvae are capable of eating as much food as they are able to eat in the laboratory. Most of the 10,978 larvae recorded are much smaller than the coprophagous muscid larvae, and the total is heavily weighted by large numbers of *Psychoda* in April, May and October (Table 17).

Table 17. *Numbers of predacious and coprophagous larvae recorded per month (neglecting secondary and occasional larvae)*

Month	Predacious Muscidae	Hydrophilidae	Coprophagous larvae
Oct.	27	0	4446
Nov.	4	1	2873
Dec.	0	2	451
Jan.	0	2	485
Feb.	0	2	757
Mar.	0	0	813
Apr.	0	24	1905
May	0	22	1390
June	30	43	1274
July	54	17	899
Aug.	34	12	873
Sept.	19	0	191

Hammer (1941) and Hafez (1948, 1949) record other species of insect acting as predators on larvae and eggs in the pat. Adult hydrophilids such as *Sphaeridium* feed on egg heaps of *Cryptolucilia* and some of the staphylinids feed on eggs and larvae (Hammer 1941). At Rothamsted the staphylinid *Aleochara languinosa* Grav. has been observed several times to feed on *Scatophaga* eggs and to pull mature *Psychoda phalaenoides* L. larvae out of the dung. *Philonthus marginatus* Strom. preys upon flies visiting the pat and has been seen catching *Psychoda*, *Sepsis* and *Copromyza* adults. The larger staphylinids probably feed mostly on larger flies and beetles. *Philonthus splendens* F. has been found feeding on *Aphodius* adults. The staphylinids were determined by Mr W. O. Steel.

The empid *Drapetis*, which breeds in the dung, has a proboscis very like that of the Asilidae and this fly has been found feeding on a small staphylinid (Laurence 1952). *Dolichopus ungulatus* L. has been found feeding on *Psychoda* larvae, pulling them from the surface of a pat in the shade. Ants of the genus *Myrmica* have been found on pats carrying fly larvae and adults.

Very often a pat is found scattered and broken up. At Harpenden this is caused by jackdaws (*Corvus monedula* L.) which nest in abundance around Rothamsted Manor. Pats in the winter have been disturbed when larvae of *Trichocera* and *Copromyza* were known to be present. In July pats have been disturbed at 6–8 days old when dipterous larvae were present. In the spring the emergence of hibernating beetles (Staphylinidae and Lamellicornia) attract the birds to fresh dung (1–2 days old), and as the beetles fly in warm weather the disturbed pat becomes too dry for larvae to develop in it. This

period also coincides with nesting of the jackdaws and almost all pats in a warm period in April were completely destroyed and rendered uninhabitable (Table 18).

Table 18. *Destruction of pats deposited between 18 and 25 April by jackdaws*

(Counted 3 May 1951)

Completely broken up	Small central area left, sides broken up	Attacked only at edges, or not attacked
93	39	21 (all more recent, deposited near the end of the warm period)

Relatively few Hymenoptera have been bred from pats, although the visitors are fairly common (Tables 19 and 20). In the summer the Braconidae and Ichneumonidae are found almost exclusively in the shade, whereas the Figitidae occur mainly on pats in the open. The most frequent species are *Phaenocarpa ruficeps* Nees, *Atractodes bicolor* Grav. and *Eutrias tritoma* Thomson?. None of these have been bred from known hosts, and possibly they parasitize the Muscidae in the pat. Handschin (1932) has recorded that the chalcid *Spalangia* is attracted only to old dung and not to fresh. The species of *Figites* and *Eucoila* appear to have similar habits in this country.

Table 19. *Adult Hymenoptera visiting cow pats*

		Age of pat in days
BRACONIDAE (det. G. E. J. Nixon)		
Phaenocarpa conspurcator Hal.	Mar., June	2–4
P. ruficeps Nees	May, July–Sept.	1–2
Pentapleura pumilio Nees	June, Aug.–Sept.	1–2
ICHNEUMONIDAE (det. J. F. Perkins)		
Atractodes bicolor Grav.	July–Aug.	1–2
A. gravidus Grav.	July, Sept.	1–2
Polyrhembia tenebricosa Grav.	Oct. (one specimen)	1
CYNIPIDAE (det. G. J. Kerrich)		
Figites consobrinus Giraud	July–Sept.	2–4
F. laevigatus Dahlb.	July	3
Eucoila boienii Hartig	Oct.	6
Eutrias tritoma Thomson?	June–July	1–2
Rhynchacis nigripes Cameron	April–May	1–2 or 68
Kleidotoma striaticollis Cameron	June–July	7
Zygosis urticeti Dahlb.	Feb. (one specimen)	35
PROCTOTRUPIDAE (det. G. E. J. Nixon)		
Exallonyx confusus Nixon	June-July	7
DIAPRIIDAE (det. G. E. J. Nixon)		
Phaenopria cameroni Kieff.	May	68
Meuselia sp.	June	? (in shade)

Tables 19 and 20 could not have been compiled without the assistance of the Staff of the British Museum (Nat. Hist.).

The flies emerging from the dung very often have mites or nematodes attached to them. Probably none of these are parasitic but utilize the fly for transport from pat to pat. *Gamasus lunaris* Berlese (det. G. O. Evans) and another gamasid have been found on adults of *Copromyza*, *Limosina* and *Sciara*. An undetermined oribatid has been found only on the Muscidae (*Myiospila*, *Hydrotaea* and *Morellia*). Hypopi of the Tyroglyphidae are commonest on Sepsidae. Hypopi on species of *Limosina* bred from

cow dung are relatively uncommon compared with those on species of *Limosina* (*ferruginata* Stenh., *pusilla* Mg.) associated mostly with horse dung. *Psychoda* carries a nematode wrapped externally between the segments of the abdomen (Satchell 1947*b*) and these have been found commonly (*Rhabditis curvicata* Schneider?). Cysts resembling the third larval stage of *Rhabditis coarctata* Leuck (Triffit & Oldham 1927) have been found on *Forcipomyia* larvae and on *Sepsis* puparia. Similar cysts, usually attached to *Aphodius*, have been found on mites in the dung. A female *Scatophaga* had the abdomen full of undetermined nematodes.

Table 20. *Hymenoptera bred from Diptera living in cow pats*

	Host
BRACONIDAE	
Pentapleura pumilo Nees	*Copromyza hirtipes* Rob.-Des.
CYNIPIDAE	
Figites sp.	*Hydrotaea albipuncta* Zett.
	H. tuberculata Rond.
Erisphagia (*Cothonaspis*) sp.	*Sepsis cynipsea* L.
DIAPRIIDAE	
Trichopria sp.	*Mesembrina meridiana* L.

Also one eucoiliform figitid larva in puparium of *Copromyza nitida* Mg.

Also emerged from pats, hosts not known:

CYNIPIDAE

Figites striolatus Hartig, *Eutrias tritoma* Thomson?, *Rhynchacis nigripes* Cameron, *Kleidotoma striaticollis* Cameron, *Erisphagia* (*Cothonaspis*) *pentatoma* Hartig.

DIAPRIIDAE

Phaenopria cameroni Kieff?

Other recorded hosts:

Species	Host	Recorded by
Phaenocarpa ruficeps	*Paregle* (Muscidae)	Séguy 1923
Atractodes	*Scatophaga*	Smith 1951
Phaenopria cameroni	*Limosina*	Goddard 1938
Figites consobrinus	*Sarcophaga*	Cameron 1889
Eucoila sp.	*Lyperosia*	Séguy 1923
Eutrias sp.	*Lyperosia* "	Séguy 1923
Kleidotoma sp.	*Haematobia*	Mohr 1943

A single *Limosina crassimana* Haliday has been found on a pat with the fruiting body of a fungus protruding through a wing vein. *Scatophaga* adults are well known to die from fungal diseases (Hobby & Elton, 1935).

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SUMMARY AND CONCLUSIONS

1. It is surprising how much an apparently efficient mammal leaves over in its faeces, sufficient to support the large population of insect, earthworm, mite, nematode and protozoan inhabitants. As well as the regular inhabitants of the cow pat the pat is also used as a shelter by other organisms such as isopod Crustacea (*Philoscia*) and

Myriapoda. Occasionally, particularly in the winter, dipterous larvae such as Tipulidae and coleopterous larvae such as Elateridae, are found in or under the pat, and probably have wandered up from the soil underneath. Old pats are occasionally colonized by ants.

2. Feeding on the animals in the pat are the internal predators, the muscid and hydrophilid larvae (2·6% of the coprophagous larvae). Staphylinid larvae live in the pat but appear to be commonest after most of the dipterous larvae have left, and some Staphylinidae are coprophagous (Hinton 1944). Also associated with the pat are the external predators ranging in size from insects, such as the small empid *Drapetis*, up to birds the size of jackdaws. Hammer (1941) records other vertebrate predators. Adult Hymenoptera frequent the pat and some species are parasitic in the larval stage on the coprophagous and predatory inhabitants. It is probable, as Hammer (1941) suggests, that the carnivorous species are important in reducing the numbers of flies associated with the pat.

3. Hammer also suggests that competition for pat material is hardly of any consequence. The numbers of larvae present, however, are much larger than formerly supposed. At certain times of the year the weight of larvae present may equal one-tenth of the sample taken. Although the numbers of larvae obtained from 1 in. cores of the pat can be very large (Table 11) it has not been possible to show that there is intraspecific competition for food without evidence of how much the larvae actually require. Krijgsman & Windred (1933) could not rear *Lyperosia* on bacterial cultures from the dung alone, but the nature of the accessory essential food material has not been determined. However, the possible number of larvae within a pat are shown to be much larger than suspected by Mohr (1943), and apparently by Hammer (1941). With reference to competition Mohr (1943) records that the beetle *Pinotus carolinus* L. may remove so much dung overnight that the pat dries out for the other inhabitants and that *Aphodius distinctus* Mueller adults, by milling on the surface of fresh dung, break up egg masses of other species.

4. Estimation of the mean numbers of inhabitants at any time is subject to error, as each pat is a discrete community and no two pats lie in exactly the same surroundings. In the larval population estimations the standard deviation of the mean of several pats in the same month was equal to the mean, whereas if the larvae were distributed at random between pats one would expect the variance to equal the mean.

5. It has been possible to show that the coprophagous community is not static. There are marked differences in the seasonal occurrence of the different species. Three groups of Diptera inhabiting the pat may be recognized, but one can make few general statements about the different species as each species behaves differently. One group occurs mainly in the summer months when the temperature is high. In contrast one group occurs mainly in the winter months and appears to be very successful at this time. A third group reaches a maximum in the spring and in the autumn, and it is suggested that these species required a greater temperature than the winter group, but also required a greater humidity than the summer group. In the summer shaded pats have a different community from pats in the open. The species which have a maximum abundance in spring and autumn possibly continue to reproduce in the shade in the summer.

6. Most of the species inhabiting cow pats have a rapid development. As well as the association of the age of the pat with different adult visitors (Handschin 1932, Hafez 1939, Hammer 1941, Mohr 1943), it is also possible to show a larval succession within the pat, conceivably associated with a fungal and bacterial succession. Such a succession has been described by Mohr (1943) in the cow pat community in America, and by Fuller (1934) in the rapidly ageing carrion habitat. Such a succession makes estimation of the total population in a cow pat difficult, especially as the age of the pat inhabited, which determines the time for sampling the larvae, depends upon the temperature and the season.

7. The lamellicorn beetles inhabiting dung are well known to act as secondary hosts to parasites of the animals producing the dung (Wehr & Lucker 1952). It is possible that the Diptera which inhabit the pat also act as hosts to the cattle parasites. Séguy (1934) refers to a record by Zwaluwenberg (1928) of eggs of the nematodes *Ascaris*, *Necator* and *Trichuris* in the abdomen of the sphaerocerid *Copromyza*. Klesov (1949) has shown that *Musca autumnalis* Deg. adults transmit keratconjunctivitis in cattle caused by the nematode *Thelazia*. The muscid genera *Lyperosia* and *Haematobia* breed in cow dung, and these genera are recorded as reducing milk yield, and in Europe and America are controlled by spraying cattle. Therefore a better understanding of the cow pat community may be of value to the agriculturist in addition to the intrinsic interest of a pat as a small rapidly evolving habitat.

REFERENCES

Baumberger, J. P. (1919). A nutritional study of insects, with special reference to the micro-organisms and their substrata. *J. Exp. Zool.* **28**, 1–81.

Bogdanov, E. A. (1901). Zur Biologie der Coprophaga. *Allg. Z. Ent.* **6**, 36–41.

Bouché, P. F. (1834). *Naturgeschichte der Insekten besonders in Hinsicht ihrer ersten Zustande als Larven und Puppen.* Berlin.

Buxton, P. A. (1936). Prolonged life of an African Stratiomyid. *Proc. R. Ent. Soc. Lond.* (A), **11**, 103.

Cameron, P. (1889). *A monograph of the British Phytophagous Hymenoptera*, III. London.

Coe, R. L. (1942). *Rhingia campestris* Mg. (Dipt., Syrphidae): an account of its life history and descriptions of the early stages. *Ent. Mon. Mag.* **78**, 121–30.

Cotterell, G. S. (1920). The life history and habits of the yellow dung fly (*Scatophaga stercoraria*); a possible blow fly check. *Proc. Zool. Soc. Lond.* pp. 629–47.

Degeer, C. (1776). *Mémoires pour servir à l'histoire des insectes*, vol. VI. Stockholm.

Duffield, J. E. (1937). Notes on some animal communities of Norwegian Lapland. *J. Anim. Ecol.* **6**, 160–8.

Emden, F. I. van (1942). Larvae of British beetles, III. Keys to the families. *Ent. Mon. Mag.* **78**, 206–72.

Fuller, M. E. (1934). The insect inhabitants of carrion, a study in animal ecology. *Bull. Coun. Sci. Industr. Res. Aust.* **82**, 1–62.

Goddard, W. H. (1938). The description of the puparia of fourteen British species of Sphaeroceridae (Borboridae, Diptera). *Trans. Soc. Brit. Ent.* **5**, 235–58.

Hafez, M. (1939). Some ecological observations on the insect fauna of dung. *Bull. Soc. Fouad. Ent.* **23**, 241–87.

Hafez, M. (1947). Further additions to the Dipterous fauna of dung in Egypt, with some biological observations. *Bull. Soc. Fouad. Ent.* **31**, 307–12.

Hafez, M. (1948). Ecological and biological observations on some coprophagous Sepsidae. *Proc. R. Ent. Soc. Lond.* (A), **23**, 99–104.

Hafez, M. (1949). Observations on the biology of some coprophagous Borboridae. *Proc. R. Ent. Soc. Lond.* (A), **24**, 1–5.

Hammer, O. (1941). Biological and ecological investigations on flies associated with pasturing cattle and their excrement. *Vidensk. Medd. dansk. naturh. Foren. Kbh.* **105**, 1–257.

Handschin, E. (1932). A preliminary report on investigations on the Buffalo Fly (*Lyperosia exigua* de Meijere) and its parasites in Java and Northern Australia. *Pamphl. Coun. Sci. Industr. Res. Aust.* **31**, 1–24.

Hennig, W. (1948–52). *Die Larvenformen der Dipteren*, Teil I–III. Berlin.

Henry, W. A. & Morrison, F. E. (1923). *Feeds and Feeding*. Madison.

Hinton, H. E. (1944). Some general remarks on the sub-social beetles with notes on the biology of the Staphylinid *Platystethus arenarius* (Fourcroy). *Proc. R. Ent. Soc. Lond.* (A), **19**, 115–28.

Hobby, B. M. & Elton, C. (1935). Mortality in the dung fly, *Scatophaga stercoraria* L. (Dipt., Cordyluridae). *J. Soc. Brit. Ent.* **1**, 71–2.

Keilin, D. (1917). Recherches sur les Anthomyides à larves carnivores. *Parasitology*, **9**, 325–450.

Keilin, D. (1944). Respiratory systems and respiratory adaptations in larvae and pupae of Diptera. *Parasitology*, **36**, 1–36.

Kettle, D. S. & Lawson, J. W. H. (1952). The early stages of British midges *Culicoides* Latreille (Diptera, Ceratopogonidae) and allied genera. *Bull. Ent. Res.* **43**, 421–67.

Kirby, W. & Spence, W. (1859). *An Introduction to Entomology*. London.

Klesov, M. D. (1949). A study of the biology of the nematode *Thelasia rhodesi* Desm. *Zool. Zh.* **28**, 515–22.

Krijgsman, B. J. & Windred, G. L. (1933). Investigations on the Buffalo fly, *Lyperosia exigua* de Meijere. *Pamphl. Coun. Sci. Industr. Res. Aust.* **43**, 4–40.

Ladell, W. R. S. (1936). A new apparatus for separating insects and other Anthropods from the soil. *Ann. Appl. Biol.* **23**, 862–79.

Larsen, E. Bro. & Thomsen, M. (1940). The influence of temperature on the development of some species of Diptera. *Vidensk. Medd. dansk. naturh. Foren. Kbh.* **104**, 1–75.

Laurence, B. R. (1952). The prey of some Empididae and Dolichopodidae (Dipt.). *Ent. Mon. Mag.* **88**, 156–7.

Massee, G. & Salmon, E. S. (1901–2). Researches on coprophilous fungi. I and II. *Ann. Bot., Lond.*, **15**, 313–58; **16**, 57–93.

Mellor, J. E. M. (1919). Observations on the habits of certain flies, especially of those breeding in manure. *Ann. Appl. Biol.* **6**, 53–88.

Mohr, C. O. (1943). Cattle droppings as ecological units. *Ecol. Monogr.* **13**, 275–98.

Portchinsky, I. (1885). Muscarum cadaverinarum stercorariarumque biologia comparata. Summary by C. R. Osten Sacken (1887). On Mr Portchinski's publications on larvae of Muscidae. *Berl. ent. Z.* **31**, 17–28.

Portchinsky, I. (1910). Recherches biologiques sur le *Stomoxys calcitrans* L. et biologie comparée des mouches coprophagues. *Travaux du Département d'Agriculture*, **8**, 1–90. Quoted by Hammer (1941) and Keilin (1917). Also *Rev. Appl. Ent.* (B) (1913), **1**, 146–8.

Réaumur, R. A. F. (1740). *Mémoires pour servir à l'Histoire des Insectes*, Tome IV. Amsterdam.

Rothamsted Experimental Station (1947). *Guide to the Experimental Farm*. St Albans.

Satchell, G. H. (1947*a*). The larvae of the British species of *Psychoda* (Diptera, Psychodidae). *Parasitology*, **38**, 51–69.

Satchell, G. H. (1947*b*). The ecology of the British species of *Psychoda* (Diptera, Psychodidae). *Ann. Appl. Biol.* **34**, 611–21.

Séguy, E. (1923). *Faune Fr.* **6**. Paris.

Séguy, E. (1934). *Faune Fr.* **28**. Paris.

Smith, K. G. V. (1951). Two Hymenopterous parasites bred from *Scopeuma stercoraria* L. (Dipt., Cordyluridae). *Ent. Mon. Mag.* **87**, 248.

Smith, V. Irwin (1920). Studies on the life histories of Australian Diptera Brachycera, Part 1. Stratiomyidae. *Proc. Linn. Soc. N.S.W.* **45**, 505–30.

Strenzke, K. (1950). Systematik, Morphologie und Ökologie der terrestrischen Chironomiden. *Arch. Hydrobiol.* (*Plankt.*), Suppl. Bd. **18**, 207–414.

Thomsen, M. (1938). Stuefluen (*Musca domestica*) og Stikfluen (*Stomoxys calcitrans*). *Beretn. Vet.- og Landbohøjsk, Kbh.* **176**, 1–352.

Thomson, R. C. Muirhead (1937). Observations on the biology and larvae of the Anthomyidae. *Parasitology*, **29**, 273–358.

Thomson, R. C. Muirhead (1947). Notes on the breeding habits and early stages of some Muscidae associated with cattle in Assam. *Proc. R. Ent. Soc. Lond.* (A), **22**, 89–100.

Tillyard, R. J. (1931). The Buffalo fly in Australia. *J. Coun. Sci. Industr. Res. Aust.* **4**, 234–43.

Triffit, M. & Oldham, J. (1927). Observations on the morphology and bionomics of *Rhabditis coarctata*. *J. Helminth.* **5**, 33–46.

Wardrop, J. C. (1953). Studies on the behaviour of dairy cows at pasture. *Brit. J. Anim. Behav.* **1**, 23–31.

Wehr, E. E. & Lucker, J. T. (1952). Insects and helminths, in Insects. *The Year Book of Agriculture*, pp. 169–79. Washington.

Westwood, J. O. (1840). *An Introduction to the Modern Classification of Insects*, vol. II. London.

Williams, C. B. (1937). The use of logarithms in the interpretation of certain entomological problems. *Ann. Appl. Biol.* **24**, 404–14.

Zwaluwenberg, R. H. van (1928). The interrelationships of insects and round worms. *Bull. Exp. Sta. Hawaii. Planters Ass.* no. 20.

THE INVERTEBRATE FAUNA OF JAN MAYEN ISLAND (EAST GREENLAND)

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(With 2 Figures in the Text)

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INTRODUCTION

Although a number of expeditions have gone to Jan Mayen (see Wordie 1922; Russell 1940*a*, *b*) the only previous studies of the animal life have been those made by the Austrian Polar Year Expedition 1882–83, the Swedish Greenland Expedition in 1899, the Cambridge University Expedition of 1921, and the Norwegian Arctic Expedition of 1930. The results of the first three are summarized by Bristowe (1925), who also quotes the taxonomic work of Edwards (1923). These earlier works will be found in the References under the names of Becher (1886) and Wahlgren (1900). Only Collembola seem to have resulted from the Norwegian expedition, and these are described by Linnaniemi (1935). With the exception of Bristowe's and Linnaniemi's work, all these papers are confined to the listing of one species of spider, fourteen of mites, two of Collembola, two Lepidoptera and nine Diptera. Bristowe's work, in addition to some useful notes on habits and zoogeography, adds four spiders, one mite, six Collembola—two of which are probably wrongly named (Gisin 1953), two Ichneumonidae, and eleven flies. Linnaniemi's paper (1935) only adds two localities for two already known species of Collembola.

King (1939) describes the general nature of an Imperial College Expedition of 1938 and papers by Russell (1940*a*, *b*) and Russell & Wellington (1940) provide an important contribution of the plant ecology of the island. Of these Russell & Wellington (1940) give general descriptions and a classification of the flora which is widely used in this paper.

The Oxford University Expedition to Jan Mayen (Marshall 1948) included two ornithologists, a botanist and the present author. J. W. Wilson, the botanist, is publishing a series of papers of which the first two (Wilson 1951, 1952) have appeared. These are not primarily concerned with general ecological problems.

The collections of soil animals described in this paper were made with two main objects in view. The first object was to describe the fauna of an arctic island governed by a rigorous climate and a 'high arctic' flora (Polunin 1951), both from an ecological and a zoogeographical point of view. The second object was to provide material for the comparison of methods of analysis aimed to distinguish the different faunistic components present in a limited region. On the continent of Europe most animal ecological work which is neither 'autecological' nor 'zoogeographical' appears to be modelled on the plant community analysis work of the Braun-Blanquet or the Uppsala schools. Papers such as those of Gisin (1943) and of Agrell (1941, 1945, 1948) and Kontkanen (1950*a*, *b*) are examples. It appeared to the present author that some investigation of the relative advantages of these methods by one who is a protagonist of neither would be useful, and also that the commonly voiced 'Anglo-Saxon' criticism, that these methods are too artificial and ignore the biology of the animals, should be investigated.

In order to avoid needless repetition in each of the specialist taxonomic papers which have already been published on the material obtained, the original collecting localities have not been separately described by each author. Section III of this paper is, therefore, the first and only full description of these localities and the same system of numbering is used in all the papers. In order that the entire flora and fauna of these localities can be visualized without reference to a number of separate journals the numerical results from all groups are brought together in Table 1.

SURVEY OF COMMUNITY ANALYSIS METHODS

The study described here was partly intended as an exercise in the techniques of faunistic analysis, as a test of whether such relatively crude methods as can be used under expedition conditions can have ecological as distinct from zoogeographical value, and whether an adequate description of the fauna of a limited arctic area can result. The methods hitherto used under such conditions fall roughly into three categories. The taxonomic naturalists have been solely interested in listing as many species as possible from the area in order to add species to those known to science and to provide material for zoogeographical studies; this work is frequently nowadays supplemented by the use of mass extraction apparatus, usually of the Tullgren type (Thor 1930, Hammer 1944, Tuxen 1944, Sellnick 1940), but on at least one occasion a flotation method has been used (Salt 1952). Secondly, the ecological approach of workers such as Elton (Summerhayes & Elton 1928) and Bristowe (1922) has involved the extensive search for outstanding faunistic differences, mainly in the dominant species, and the relation of these to vegetational, physical and biotic influences by that combination of observation and inspired common sense which is the peculiar province of the good naturalist. Thirdly, there has sprung up in the last twenty years a type of work in which it is attempted to make such studies more 'objective' by the use of a

combination of quantitative sampling and numerical methods of analysis the 'subjective impressions' of the naturalist usually being eschewed. This originated from the botanical work of Braun Blanquet on the one hand and the Scandinavian plant sociologists especially at Uppsala on the other, and has been applied to animal ecology by various workers, of whom the main protagonists of the two schools are Gisin (1943, 1949) and Agrell (1941, 1945, 1948); other Scandinavian workers are Renkonnen (1938) Kontkanen (1950*a*, *b*) and Sørensen (1948), while Tuomikoski (1942) gives a valuable review from the opposite point of view.

From the point of view of faunistic analysis the main tool of the Scandinavian school is the 'trellis diagram' which is a two-dimensional coincidence table with the samples arranged linearly along two sides at right angles. The squares where rows and columns meet contain numbers which represent the extent to which the faunas in the two localities are similar. All possible combinations of pairs of localities are assigned such correlation coefficients, which are calculated by different workers on a wide variety of principles, different degrees of importance being attributed to dominance and constancy and abundance (Kulczynski 1927, Renkonnen 1938, Sørensen 1948, Kontkanen 1950*a*, *b*). The order of the samples along the sides of the tables is then rearranged, mainly by trial and error, so that those samples which are most similar in their fauna are brought nearest to each other as indicated by the highest correlation numbers approaching the central diagonal line of the table. Such tables can be used to arrive at a linear order of affinity of both localities and also of species, thus growing together those species with similar ecological affinities. An example of such a table worked out for the Jan Mayen Collembola is given in Fig. 1.

The method of Gisin (1943, 1947, 1951) is a less rigid one; by inspection of the results obtained from sampling, certain species are found to be 'vicariants'. It is worth quoting here a number of definitions: Gisin (1947) defines *vicariant* species as 'd'espèces qui ne cohabitent jamais, qui se remplacent mutuellement ou...dont l'affinité cénotique est nulle. D'autres espèces cohabitent quelquefois, mais jamais en nombre simultanément, leur vicariance est relative, leur affinité cénotique faible'. Elton (1927) states that 'species which occur in particularly large numbers (in one zone) although they are not exclusively confined to it...these we call *characteristic* species'. Tansley (1923) defines *exclusive* species as those which are confined to one community, *characteristic* species as those which are commoner within the community than without it, and *constant* species as those which are present in every example, or nearly every example, whether met with outside or not. The term *indicator species* is usually used in Europe to mean a species associated with a particular feature of the physical environment. In view of the slight difference of meaning from Gisin's vicariant species, Gisin's own renunciation of the term (1951), and the unpopularity of this term in Britain, it has been decided to refer to the species chosen as indicating the ecological boundaries of the Jan Mayen faunistic types as *differential* species and to define these as species which are constant in all examples of a particular association of species (here called a *fauna*) and are mainly confined to that association. I am grateful to Dr Gisin for his advice on this point. Constancy is defined rigidly as being present in 80% or more of samples in a sampling locality. Constancy is rated as more important than exclusiveness, so that only one of the differential species selected is in fact

	Archisotoma besselsi	*Neelus minimus*	*Pseudanurophorus binoculatus*	*Willemia anophthalma*	*Xenylla humicola*	*Hypogastrura succinea*	*Sminthurinus concolor*	*Tullbergia arctica*	*T. krausbaueri*	*Onychiurus debilis*	*O. arcticus*	*Anurida remyi*	*Folsomia sexoculata*	*F. bisetosa*	*Onychiurus macfadyeni*	*Micranurida pygmaea*	*Isotoma notabilis*	*Isotomiella minor*	*Folsomia sensibilis*	*Isotoma viridis*	*Onychiurus groenlandicus*
Archisotoma besselsi	100	×	×	·	×	·	×	·	×	×	·	·	×	×	×	·	×	×	·	·	·
Neelus minimus		100	√	·	×	·	×	·	×	×	·	·	×	×	×	·	×	×	·	·	·
Pseudanurophorus binoculatus			100	·	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Willemia anophthalma				100	·	·	·	·	·	·	·	·	·	·	·	·	×	·	·	×	·
Xenylla humicola					100	58	√	57	42	√	√	√	33	42	35	·	11	√	√	16	√
Hypogastrura succinea						100	√	50	35	√	·	√	56	35	30	·	·	·	√	√	·
Sminthurinus concolor							100	×	×	√	·	·	√	×	×	·	×	·	√	×	×
Tullbergia arctica								100	35	×	×	·	28	35	30	·	√	·	√	35	×
T. krausbaueri									100	35	·	×	38	20	45	×	√	√	√	√	·
Onychiurus debilis										100	75	·	56	35	30	·	·	·	√	×	×
O. arcticus											100	·	53	60	55	·	·	·	·	·	·
Anurida remyi												100	53	·	55	·	·	·	·	60	·
Folsomia sexoculata													100	38	47	√	10	28	53	25	√
F. bisetosa														100	60	·	√	35	60	20	·
Onychiurus macfadyeni															100	√	24	30	55	30	×
Micranurida pygmaea																100	×	·	×	·	·
Isotoma notabilis																	100	32	√	√	·
Isotomiella minor																		100	75	35	·
Folsomia sensibilis																			100	60	·
Isotoma viridis																				100	√
Onychiurus groenlandicus																					100

Fig. 1. Affinities of Collembola according to trellis-diagram method.

completely exclusive (*Pygmephorus spinosus* in Fauna 6). On the other hand, all the differential species are constant with minor exceptions in Faunas IV and VII which are due to very impoverished sampling localities. It is not claimed, of course, that such a definition is more than a guide to the exercise of 'enlightened common sense'; to expect otherwise would be to ignore the considerations listed at the end of this section. By judicious selection of differential species it is possible to divide up the whole range of samples into those characterized by certain species, the confidence to be placed in such a classification being reinforced as the ranges of several differential species can be shown to conform to the same system.

Any method by which many samples are to be classified according to their fauna should take account of the following features:

(1) No existing soil sampling method is quantitatively reliable for all groups of animals (Macfadyen 1953); therefore the results must not be unduly influenced by inaccuracies in the figures obtained. This could happen with some methods of calculating correlation coefficients in trellis diagram work.

(2) The method must not be unduly influenced by the occasional presence of accidental species, nor should the presence of ubiquitous species with very wide distributions obscure the results.

(3) When the sampling has been carried out with only a single size of sample, some species will inevitably occur in large numbers in almost every sample while others will be quite sporadic even when at their maximum density, because the density of samples is greater than that of the animal. Predatory mites tend to fall into the latter category in the Jan Mayen material. Methods of calculation based on 'constancy numbers' cannot be used in such cases, and allowance for varying natural densities must always be made.

(4) It is not possible when sampling an unexplored region for the first time to arrange for the sampling of all faunistic types to produce similar numbers of animals, because these are the unknown factor. One can only cover a wide range of vegetational and physical factors, sampling sites being selected on a partly arbitrary basis, and hope to include most faunas. Thus any rigid methods which tend to bias the observer towards creating faunas with approximately equal numbers of samples should be avoided.

(5) Both the selection of sampling points and also the interpretation of results should be as independent as possible of the judgement of the ecologist. Agrell made extensive claims for the objectivity of his methods of analysis, which are justified, but he has been justly criticized by Gisin on the grounds that, in practice, his methods of sample site selection are not objective, but follow already determined vegetational classifications. Obviously complete objectivity in this sense can only be achieved by the random selection of sampling points spread over the entire area under study, an impracticable procedure when an area of any size is to be covered. In the case of the Jan Mayen sampling, objectivity was only achieved to the extent that many sites which were not thought likely to have any fauna were sampled (often a rewarding procedure, since very few totally barren samples were found). The actual point of taking the samples was determined by throwing a marker where practicable, and all places where slight variations of physical and vegetational conditions could be detected were sampled.

The Jan Mayen samples were taken in groups of five *sampling units* so that both a

mean, representative of the whole apparently uniform area chosen, could be calculated and also some estimate of the *frequency* of each species could be made. In the interpretation of results animals present in four or five of the five sampling units are called *constant* (bold-face type in Table 2), those in two or three of the five *present* (italics in Table 2) and those in one sample only *casual* (plain type). Animals whose total abundance in the five sampling units is less than five individuals are marked with a cross.

An impartial attempt was made to apply independently the Scandinavian trellis diagram method of analysis and the 'method of correlations' of the Swiss school in turn. Each of the four main taxonomic groups (Parasitiformes, Trombidiformes, Oribatei and Collembola) was treated separately at first. It would be pointless to reproduce here all this work. Suffice it to say that the trellis diagram proved too cumbersome, too insensitive owing to the large number of ubiquitous species and the lack of discrimination against them, and made one extremely conscious all the time of the artificiality of trying to arrange in a linear series a set of samples obviously linked by a large number of independent relationships. However, once the idea of differential species had been applied to discriminate between the ubiquitous and the restricted but locally consistent species, a general division of the seventy-five localities into a number of groups was possible. When this was done with each of the taxonomic groups separately, and the samples were arranged linearly within each faunistic group, two features were apparent: the same general system could be applied to all four taxonomic groups, and different taxonomic groups tend to exploit different locality groupings to different extents. Thus what came to be labelled the type II fauna (*Xenylla humicola–Onychiurus debilis* community of bird cliffs) is mainly the province of Collembola while the type V fauna (*Oribatula crassipes* community of drier Phanerogam-dominated areas) is that of Oribatei. The Prostigmata, although mainly widespread and present in low densities, dominate in the type IV fauna (*Zercon curiosus* community of fjaeldmark).

A too rigid application of numerical rules to such methods leads to difficulties owing to the inherent barrenness of some types of locality and richness of others and also to the natural variations in density of different groups mentioned in point (3) above, and the varying efficiency of extraction mentioned in point (2). Thus numbers which would indicate a constant in one locality should be interpreted as meaning a casual in another, because sampling methods are imperfect, and because animal numbers are constantly, as a result of migration, mortality and replacement, fluctuating greatly both in space and in time. Thus samples with essentially the same qualitative composition but with quite large differences in numbers must be regarded as belonging to the same fauna. For example, fauna V contains a number of 'dilute' samples (S 1, S 5, S 6). Had it been possible to sample each locality weekly for a whole season, as was done for 5 weeks in the case of B 2, with rather informative results (see p. 291), a closer approximation to the characteristic fauna of each locality might have been achieved.

This consideration, in particular, appears to the author to be the overwhelming objection to the use of methods such as that of the trellis diagram which, while they may apply well enough to the distribution of relatively static organisms such as plants, appear to be far too rigid in their application to animal populations. When applied to comparisons *within* one faunistic type, as for example between the fourteen localities of fauna II, such a method allows one to re-arrange the samples according to an

apparent order of affinity. However, there seems to be little certainty even here that the same order would be arrived at in a number of succeeding weeks when, for example, a predator population had transferred its attentions from one place to another, or a particular group of nymphs had become adult. Further, as Braun-Blanquet pointed out (1932, p. 58), the mere replacement of one dominant species by another should not be regarded as a reason by itself for recognizing two distinct community types. Only in the case of a series of rather similar localities in which a single dominating physical factor is paramount does this method appear to give consistent results. This is partly true of the fauna IV localities, which range from rather dry to rather wet, and to some extent bridge the gap between fauna II and fauna V.

A rather more satisfactory and much less laborious substitute for the trellis diagram method is due to Prof. Kühnelt who kindly demonstrated this method to the author. By simply rearranging the rows and columns of a figure such as that of Table 2, with the aid of scissors and paste much can be done to group species and localities together which have the closest affinities. This can hardly be done with an extensive material such as the present one without some preconceptions about the groups, however, and in fact seems to be best used in conjunction with the criteria of vicariant or differential species. By itself it suffers from many of the objections which apply to the trellis diagram method, and the author is not inclined to attach much significance to the precise order in which the localities are arranged in Table 2, for instance. Certainly the Jan Mayen results owe what value they have mainly to the use of the differential species method.

A number of other combinations of methods were tried, including the plotting in two dimensions of a linear arrangement derived by the above techniques against a scale representing the number of indicator animals present in each locality. This breaks down the rigidity of the linear series and brings the impoverished localities together. By drawing contours representing the various physical factors on such 'maps' it is found that the localities having much soil water, those influenced by salt water, fouling, coarse sand particles, etc., form groups together and that the general pattern conforms well to that of the vegetation types. However, it was decided that most of this information could be obtained by inspection and that Table 2 represents the most useful type of analysis.

METHODS

The apparatus used to extract the soil fauna was the 'expedition funnel' apparatus described elsewhere (Macfadyen 1953). This is a multiple (30-sample) Tullgren type funnel in which heat is derived, via a water-bath, from a paraffin stove. It should be stressed that all the soil fauna counts given are minimal. It is unlikely that the catches represent much more than 50% of the numbers present in the soil for any groups other than the adult large Oribatei; even these may be low, and the Prostigmata in particular, which are represented erratically and sparsely in the samples, may be grossly underestimated. In any future investigation of this kind an apparatus incorporating Haarløv's (1947) principle for preventing condensation should be used.

Cores were taken in stainless steel tubes 10 cm.^{2} in cross-section and 5 cm. long, wrapped in paper and placed in the apparatus within a few hours (except in the case

of the S series, in which a day's boat journey and the fact that forty-five samples were taken necessitated longer delays). Wider and shallower samples would be preferable in that they would allow more rapid and complete drying and larger samples in the poorer localities. Extraction lasted for 2 or 3 days, depending on moisture content, and it was shown in a number of tests that not more than 10% more animals came out after this period. Again, a greater extraction capacity/sampling rate would be needed for a more accurate estimation of numbers. The samples were returned to England in 80% alcohol. In a few cases, notably some of the C and Q series samples, the very sandy soil resulted in much sand entering the samples. It was found possible to separate this heavy sand from the light animals by a simple flotation technique also described elsewhere (Macfadyen 1953).

The sampling continued over a period of 5 weeks, and during this time weekly samples were repeated in one locality (B 1). The results of this test, presented on p. 291, show that in this one site the fauna was not constant during this period, and that precise details of faunistic differences when comparisons are made between different localities should be interpreted with this in mind. Sets of five sampling units were taken irregularly spaced within each locality. There were seventy-five localities and therefore 375 such subsamples (hereafter called sampling units in deference to statistical usage). Each locality is given a code name which has no special significance beyond the fact that those with the same letter come from the same geographical locality and were taken on the same day. All the figures given in Table 2 and used for comparison throughout this paper are the averages of the figures from the five sampling units; the original data are too voluminous to publish but are held at the Bureau of Animal Population.

On return to camp samples were weighed and then reweighed after extraction of the fauna and drying to constant weight at 100° C. This 'measured moisture content' is probably a reasonable estimate of the water retaining capacity of the soil because rain fell on nineteen out of the thirty-five days of the sampling and the relative humidity was below 90% for only twenty-one and below 80% for three of the 6-hr. meteorological readings taken during this period. However, no allowance was made for variable amounts of above-ground vegetation present in the samples, a fact which makes interpretation difficult in some cases.

When the samples were taken, records were made of the following features, which are presented in this order in Table 1:

VEGETATION GROUP NUMBER as given by Russell (1940*a*) and briefly summarized:

Type		Type	
1	Lava fields	14	Moist earth slides
2	Exposed hillsides, dry moss	15	Screes and moraine slopes
3	Exposed hillsides, wet moss	16	Late snow areas
4	Moist slopes of weathered basaltic tuffs	17	Moist alluvial gravel beds
5	Open rocky ground	19	Faces of bird cliffs
6	Volcanic desert	20	Slopes below bird cliffs
7	Sandy beaches	21	Arctic fox burrows
8	Edges of streams and pools	22	Human habitations
9	*Sibbaldia* banks (the 'highest' vegetation on the island)	23	Bare mountain tops (this is added by the present author).
10	Consolidated hollows in lava fields		

FAUNISTIC GROUP NUMBER, as derived in section II *d* (p. 277) of this paper and containing differential species as follows:

1*a* *Oppia neerlandica* community of shore vegetation
1*b* *Archisotoma besselsi* community of the sea shores
2 *Xenylla humicola–Onychiurus debilis* community of bird cliffs
3 *Onychiurus groenlandicus* community of non-fouled damp places
4 *Zercon curiosus* community of fjaeldmark and similar areas
5 *Oribatula crassipes* community of drier Phanerogam-dominated areas
6 *Pygmephorus spinosus* community of grassy areas
7 *Microtydeus subtilis* community of exposed barren areas

SUBJECTIVE DRYNESS INDEX, 0 (dry) to 5 (very wet) based on impression of dampness in the field.

MEASURED MOISTURE CONTENT (indicates water retaining capacity), 0 (dry) to 5 (very wet); the following code is used:

0– 9% water = code no. 0	30–39% water = code no. 3
10–19% water = code no. 1	40–49% water = code no. 4
20–29% water = code no. 2	50–100% water = code no. 5

PLANT MATTER, as a percentage of total soil content.

DOMINANT PARTICLE SIZE, 1 (very coarse) to 5 (very fine).

EXPOSURE, estimated in the field, 1 (fully exposed) to 5 (well sheltered).

ALTITUDE in metres.

MAP REFERENCE (see Fig. 2) followed by locality notes.

Notes on geology, dominant plants* and biotic factors.

DESCRIPTIONS OF SAMPLING LOCALITIES

The following descriptions are supplementary to the data given in Table 1, in which a number of physical and floristic characteristics are tabulated. The meanings of the various code numbers are given above, and the map references apply to Fig. 2 (eastings before northings). The division of the Nematoda into biological groups is based on the work of Overgaard-Nielsen (1949). Since his generalizations about feeding do not necessarily apply to the same species as found on Jan Mayen, the table should be regarded as giving only a very general indication of the feeding habits of this group. The letters in the column for aphidae are the initial letters of the generic name: M = *Myzodium rabeleri*; C = *Cavariella aegopodii* (Scopoli); K = *Kakima saxifragi* Doncaster & Stroyan 1952.

A1. Volcanic desert, olivine sand 'soil', plants in hollows. Samples in tussocks of *Carex incurva*.

A2. Adjacent to A1, in tussocks of *Poa alpina* var. *vivipara*.

A3. Adjacent to A1, in tussocks of stunted *Oxyria digyna*.

A4. Edge of a cave in the volcanic desert; feathers and detritus tend to collect in the caves which are dark and damp; a fairly rich flora develops on the edge of the cave including, besides the three species above, *Cerastium alpinum*, *Ranunculus glacialis*, *Saxifraga groenlandica*, *S. nivalis*, *Cochlearia officinalis*. Here samples were taken.

* It is most unfortunate that the author's collection of mosses was lost by the expert to whom they were sent for identification. A general idea of the moss fauna can be obtained from the paper of Russell (1940*a*).

Table 1. *Soil fauna samples: explanation on pp. 268 and 281*

Station number	Vegetation type	Faunistic type	Subjective dampness	Measured moisture	Plant matter	Dominant soil particle size	Exposure	Altitude (metres)	Open	Vegetation: Mosses	Vegetation: Lichens	Vegetation: *Salix herbacea*	Vegetation: Flowering plants	Vegetation: Grasses	Fouling	Marine influence	Map reference	Animals: Fly larvae: *Smittia*	Animals: Fly larvae: Lycopiidae	Animals: Fly larvae: *Metriocnemus*	Animals: Enchytraeidae	Animals: Aphidae	Animals: Nematoda: Bacteria-feeding	Animals: Nematoda: Plant-feeding	Animals: Nematoda: Predatory
S 9	7	1*a*	1	.	1	3/4	2	0	×	.	.	.	×	.	.	×	0303	.	.	.	1	.	.	.	.
C 1	.	1	2	0	0	4/3	2	0	×	.	.	.	.	.	.	×	5963	.	.	.	.	.	.	.	.
C 3	.	1	1	.	.	4/3	3	0	×	.	.	.	.	.	.	×	4773	.	.	.	.	.	.	.	.
B 8	20	2	4	2	.	.	3	30	×	×	.	.	×	×	×	.	4456	.	×	.	.	.	×	×	.
B 5	20	2	2	1	.	.	4	40	.	×	.	×	.	.	×	.	4455	.	.	.	.	m	×	×	.
B 13	20	2	2	2	.	.	3	20	×	×	.	.	×	×	×	.	4557	×	×	.	.	.	.	.	.
B 7	20	2	5	4	.	.	3	60	.	×	×	.	×	×	×	.	4456	×	×	×	.	.	×	×	.
Q 7	20	2	5	4	.	.	4	0	×	×	.	.	.	.	×	×	4773	.	.	×	31	.	×	.	×
B 9	20	2	5	3	.	.	4	30	.	×	.	.	×	×	×	.	4556	.	×	.	.	.	×	×	.
B 3	20	2	3	1	.	.	5	25	.	.	.	.	×	.	×	.	4555	×	.	×	2	.	×	×	.
B 10	20	2	3	1	.	.	3	50	.	×	.	.	×	×	×	.	4455	×	×	.	.	.	×	×	.
B 4	20	2	3	0	.	.	5	40	.	×	.	.	×	×	×	.	4455	×	×	.	.	k	.	×	.
B 2	20	2	3	2	7	4/5	4	5	.	.	.	.	×	×	×	.	4555	.	.	.	1	.	×	×	.
B 1	21	2	3	0	.	.	4	5	.	.	.	.	.	×	×	.	4555	.	.	.	.	.	×	×	.
B 11	19	2	5	1	.	.	5	20	×	.	.	.	×	.	×	.	4555	.	.	.	33	k	×	×	.
B 12	19	2	5	1	.	.	5	20	×	×	.	.	.	.	×	.	4555	.	.	.	15	k	×	×	.
D 1	17	2	1	0	0	4/5	2	0	×	.	.	.	×	.	?	.	4761	.	×	.	1	.	×	×	.
H 1	8	3	5	4	18	3/4	3	3	.	×	.	.	.	.	.	.	5268	.	.	.	.	.	.	×	.
N 3	8	3	5	5	14	3/4	5	20	.	×	.	.	.	.	.	.	9898	.	.	.	.	.	×	×	.
A 3	6	4	3	2	.	.	5	0	×	.	.	.	×	.	.	.	5053	.	.	.	.	.	×	×	.
E 3	6	4	3	2	.	.	3	0	.	×	.	.	.	.	.	.	5278	.	.	.	.	.	.	×	.
E 2	17	4	2	2	.	.	3	0	.	×	.	.	.	.	.	.	5278	.	.	.	.	.	.	.	.
E 4	17	4	4	3	.	.	3	0	.	×	.	.	.	.	.	.	5378	.	.	.	.	.	×	.	.
E 6	17	4	4	3	.	.	3	0	.	×	.	.	.	.	.	.	5379	.	.	.	.	.	×	.	.
J 4	15	4	1	5	.	.	4	10	×	×	×	.	.	.	.	.	5375	.	.	.	.	.	.	.	.
F 4	16	4	5	5	36	5/4	4	100	×	×	.	.	.	.	.	.	4763	.	.	.	.	.	.	×	.
H 2	8	3	5	4	14	3/4	3	20	.	×	.	.	.	.	.	.	5268	.	.	.	.	.	.	×	.
E 1	17	4	1	1	0	5/4	3	0	.	×	.	.	×	×	.	.	5278	.	.	.	.	.	.	.	.
E 8	17	4	3	2	.	.	3	0	.	×	.	.	.	.	.	.	5278	.	.	.	.	.	.	.	.
Q 6	23	4	0	0	0	4/2	1	150	.	×	.	.	×	.	.	.	4772	.	.	.	.	.	.	.	.

| | | |

A 5. Bare slabs of ropy lava without soil in the lee of the escarpment to the N.W. of the South Lagoon; samples taken in small mounds of moss spreading from cracks.

B series. All this series was taken in the immediate neighbourhood of The Pillar (M.R. 4556) which is the nesting place of many sea birds, especially Fulmar petrels. As the rock itself is an agglomerate mass the mineral status of the soil may be fairly high. Localities on the south side (B 1 to B 6 and B 10 to B 12) are sheltered and warm, while those on the north side are much colder and wetter. B 4, 5, 6, 7, 8, 10 and 13 showed little sign of direct fouling by the birds, but

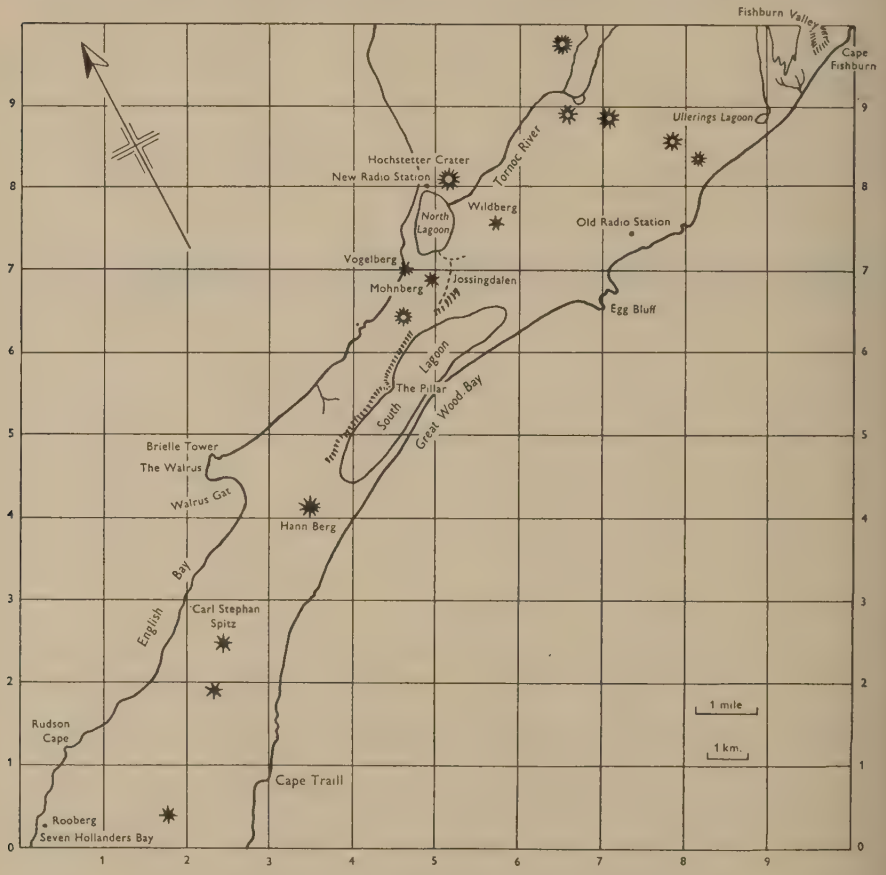


Fig. 2. Sketch-map of central Jan Mayen to show sampling sites.

even so would doubtless benefit to some extent. The relatively dry, sheltered and non-fouled places, B 4, B 5 and B 10 have a flora approaching that of the more 'advanced vegetation' of Fishburn Valley (N series) and Seven Hollanders' Bay (S series). B 13 is distinct in having an open vegetation on a recolonized landslip while B 1 is at the mouth of the burrow of an arctic fox where the dominance of grasses indicates a high nitrogen status.

B 1. Samples in *Poa alpina* var. *vivipara* near fox's earth.

B 2. *Festuca rubra* with some *Oxyria digyna*, *Cerastium alpinum* and *Poa alpina*. Bird influence probably stronger than B 1 and a more organic soil present.

B 3. Pure *Oxyria digyna*, merging into *Poa* and *Festuca* and *Saxifraga rivularis* at the edges. Similar to B 2 with, perhaps, less bird fouling.

B 4. Approximately two-thirds of the way up the saddle joining the Pillar to the escarpment;

*Taraxacum croceum** with *Saxifraga cernua*, *Poa alpina* var. *vivipara*, *Cerastium alpinum*, *Festuca rubra*, mosses.

B5. Similar to B4, with *Salix herbacea*, *Rhacomitrium* moss, *Saxifraga nivalis*, *S. cernua* and *Cerastium alpinum*. This merges into the vegetation of D1.

B7. North-east face of the same ridge with very deep wet moss and *Luzula confusa* and a foliaceous lichen.

B8. Lower and more east-facing site than B8, a recolonized landslide with moist vegetation but a porous soil. Mosses, *Poa pratensis*, *Oxyria digyna*, *Saxifraga rivularis*, *S. groenlandica*, *S. nivalis*, *Cerastium alpinum*.

B9. Very damp and fouled area at foot of cliff; *Poa pratensis* and moss with *Saxifraga rivularis*, *Festuca rubra*.

B10. Similar to B4, but more exposed; *Saxifraga cernua* with *Poa vivipara* and *Saxifraga rivularis*.

B11. Crevices in the rock of the cliff which streams with water. *Saxifraga rivularis*.

B12. Adjacent but under a ledge and with moss only.

B13. Near B8, a recent landslide with an open vegetation of the same plants.

C1. The spit of sand dividing the South Lagoon from the sea; no vegetation, but drying seaweed and a litter of stranded crustacea provide organic matter.

C2. The same but not under seaweed. No fauna found.

C3. A pebbly beach at the foot of the Vogelberg, just above high-water mark. *Neomolgus littoralis* caught by hand in this area.

D1. Beds of coarse red and black gravel at the north shore of the (sea-water) South Lagoon. Samples in scattered *Ranunculus glacialis* plants. These samples may have been fouled by the bird cliff of the B area.

D2. The same but in *Cochlearia officinalis* plants.

D3. The same, but the gravel between the plants.

E1. In the delta of the Tornoe river at the North Lagoon. The valley runs E.N.E.–W.S.W. and is rather sheltered and dry once the spring snow-melt is over. Samples taken in a flora of *Luzula confusa*, *Salix herbacea*, *Cerastium alpinum*, *Oxyria digyna Ranunculus glacialis* and moss on an alluvial gravel soil.

E2. Similar but damper and sandier and with a purple moss vegetation.

E3. Similar but slightly damper and with a yellow *Rhacomitrium* moss vegetation.

E4. Similar but slightly damper and with red *Rhacomitrium* moss, apparently the same species.

E5. Similar to E1, very damp lake shore of a coarse olivine sand, no vegetation, but some detritus and bird feathers.

E6. Similar to E4, higher up the delta in a stream bed.

E7. Similar to E5, but finer sand.

E8. Similar to E5, but drier and covered with a continuous carpet of yellow *Rhacomitrium*; this verges into the L type localities but is more protected from wind.

F1–4. These are a series of non-quantitative samples taken in the detritus on and around the snow of a late snow pocket in a cleft in the scarp above the South Lagoon; all have similar features and a greatly impoverished fauna, only at all numerous in F4.

H1. Stream at southern end of Jøssingdalen with a bed of slaty stones and sand; sample in moss at water's edge.

H2. As H1 but in totally submerged moss.

J1. Boulder scree at the base of Wildberg mountain on the Tornoe delta (north) side. Samples in lichen on the boulders.

J2. As J1, but in pockets of 'soil' consisting of gravel and detritus under rocks.

J3. As J1, but samples in clumps of *Rhacomitrium* moss among the lichen.

J4. As J1, but samples in lighter coloured *Rhacomitrium* forming a complete carpet on the tops of some ridges.

K1. A somewhat sheltered hillock at the foot of Mohenberg, facing S.E. in Jøssingdalen. Appearing very dry and with a dry vegetation which is presumably the nearest approach to the formation of '*Sibbaldia* banks'. Slope rather gradual. Samples in dry lichen with some *Saxifraga oppositifolia*. Probably considerable solifluxion, and conforming to the 'terraces' described by Wilson (1952).

* This specific name is open to some doubt (Wilson, personal communication).

K2. As K 1 but farther downhill, *Stereocaulon alpinum* lichen with some *Oxyria digyna*, *Festuca rubra*, *Cerastium alpinum*, *Luzula confusa*, *Salix herbacea* and mosses.

K3. As K 1, but farther downhill, samples in mats of *Salix herbacea*.

K4. As K 2, with similar plants but with yellow *Rhacomitrium* abundant, farthest down the slope.

L1. Loose slaty stones with sand and gravel between in the bottom of Jøssingdalen. This region is rather less developed but essentially similar to that studied by Wilson (1951), and samples were taken in conjunction with him. L 1 were in the brown, weathered region of the *Rhacomitrium* clumps and, as will be seen, have a much poorer fauna.

L2. Similar to L 1 but samples in the green, healthy *Rhacomitrium*.

L3. Similar to L 1, but samples in the interstitial sand and gravel.

N series. All these samples were taken in or around the Fishburn Valley where, as Russell (1940*a*) discovered, the *Sibbaldia* banks have their greatest development. He attributes this to 'shelter from wind, adequate moisture supply, good drainage and accumulation of soil; the most luxuriant growth occurred on banks facing south'. No animal influence appears to be at work, although Wilson (private communication) has demonstrated that potash and phosphate are more plentiful in such places. The soil is almost 'clayey' to touch and with well-developed humus.

N1. In a *Sibbaldia* bank in the valley itself.

N2. Almost vertical basalt cliff facing S.E. below the valley and beside a small waterfall. Very rich vegetation including *Taraxacum croceum* (where samples were taken) with *Veronica alpina*, *Sibbaldia procumbens*, *Saxifraga nivalis*, *S. cernua*, *Cerastium alpinum*, *Arabis alpina*, *Oxyria digyna*, *Poa alpina*, *Festuca vivipara* and *F. rubra*, *Trisetum spicatum* and other plants. This is zone 11 of Russell & Wellington (1940, p. 174).

N3. As N 2, but in dense damp moss beside the waterfall.

N4. As N 2, *Salix herbacea*, forming a continuous drier carpet farther down the slope.

N5. On a moraine ridge, to the S.W. of Fishburn Valley, separating it from the south glacier facing S.E. Loose stones and gravel, covered by a *Rhacomitrium* carpet with occasional hollows containing *Empetrum hermaphroditum*, where samples were taken. This type is mentioned by Russell & Wellington (1940), but is included in type 5.

N6. In Fishburn valley; *Salix herbacea*, *Equisetum arvense* and *Rhacomitrium* at the foot of a *Sibbaldia* bank.

Q series. With the exception of Q 7, these samples were taken near the top of Vogelberg, a craggy mountain of porous ashy volcanic rock, with an agglomerate core. It was noticed that spiders were abundant in a particular type of crevice in laminated brown rock and that *Onychiurus macfadyeni* and *Folsomia sexoculata* abounded there despite the very exposed position and lack of vegetation. Besides a direct count of twenty-five spiders, one mite and twelve Collembola in a square metre, sample Q 5 was taken here. The remainder were taken nearby.

Q1. Moss on brown volcanic ash.

Q2. Bare soil under volcanic rocks, near Q 1.

Q3. Bare gravel. Near Q 1.

Q4. Tussocks of *Saxifraga groenlandica*. Near Q.

Q5. Peculiar flaky brown volcanic stone where spiders lived.

Q6. Dark blue coke-like volcanic ash on NE. side of Vogelberg peak with a sparse, open vegetation of mosses, *Ranunculus glacialis*, *Oxyria digyna*, *Saxifraga groenlandica*, in which spiders were only about one per square metre.

Q7. At the foot of Vogelberg, and beneath a kittiwake gull colony right on the sea beach; differs from the B series bird cliff sites in having sea-water influence. Some moss, otherwise no plants, but much organic detritus and birdlime. Enchytraeid worms and *Xenylla humicola* very evident to the eye.

S series. All samples taken in the vicinity of Seven Hollanders Bay, in the south of the island; S 2, S 3, S 4 were in Russell & Wellington's (1940) 'consolidated hollows in larva fields' where a less luxuriant *Sibbaldia* flora occurs; the remainder cover a variety of localities.

S1. Very large, lichen- and *Rhacomitrium*-covered boulders of lava behind the bay with very good drainage but feeling damp to the touch. Samples in the lichen.

S2. Rather poor *Sibbaldia* banks.

S3. *Taraxacum croceum* with some *Salix herbacea* on the more south-westerly banks.

S4. *Myurella* moss in the floors of the hollows.

S5. In the lava flow to the north of the bay are large patches covered with gravel; samples taken in large clumps of pure white lichen.

S6. Gravel pockets in a wide expanse of *Rhacomitrium* moss on a hilltop to the S.E. of the bay. Samples taken in the gravel, where spiders were found.

S7. The rocky bank of a small protected hanging valley a few hundred metres to the N.E. of the bay, near the sea. A carpet of *Salix herbacea* with some *Equisetum arvense* and lichens, facing S.E.

S8. The damper, N.W.-facing bank of the same valley with moss and some *Poa pratensis*.

S9. Foreshore of the bay, just above high-water mark. *Halianthus peploides* clumps which tend to accumulate detritus and are subject to salt-water influence.

V series. These are four patches of *Poa*-like grass growing in Jøssingdalen and, in view of the opinions of Russell & Wellington (1940) and Summerhayes & Elton (1928), 'that grasses are associated with high nitrogen content' probably owing their existence to human refuse from the camps which were occupied in the 1939–45 war. Wilson (personal communication) has confirmed high nitrogen content in the V 2 sample locality. The surrounding habitat is that of the L and to a lesser extent the K series of samples. In all these sites human fouling is probable.

V1. Near the war-time radio station.

V2. A thin grass carpet on a sandy soil above a large rubbish dump near the bottom of the valley and the North Lagoon.

V3. Luxuriant tussocks in the stream bed on sandy soil; damper; near the large barrack hut* in a subsidiary valley at the foot of Wildberg.

V4. A bank of gravel and sand by the stream bed near the war-time radio station, very sheltered and rather damp, facing SE. and probably dug when the hut was constructed. *Taraxacum croceum*, *Salix herbacea* and grass present.

THE ECOLOGICAL COMMUNITIES AND THEIR DISTRIBUTION

The association of particular animals with particular physical and vegetational factors is mentioned on pp. 281–91 and will also be apparent from the characteristics of the relevant fauna type. No detailed analysis of the effects of such factors is therefore given in this section. On the other hand, it will be evident from Table 1 that there are correspondences between the general features of the sampling localities and the type of fauna found there. In this section, first the influence of each type of factor is considered in turn, then a brief description of each faunistic type is attempted and then communities described by other authors are compared with those derived here.

(*a*) *The influence of vegetational and physical factors on the fauna*

Fauna type VI directly corresponds with part of Russell & Wellington's vegetation type 22 (the vicinity of human habitations). Fauna type II*b* (samples B 11, B 12, B 13) is equivalent to vegetation type 19 (faces of bird cliffs) plus type 14 (moist earth slides), the latter having an impoverished version of the fauna of the former. Fauna type II*a* (samples B 1, B 2, B 3, B 4, B 5, B 7, B 8, B 9, B 10, Q 7) is directly equivalent to vegetation type 20 (slopes below bird cliffs), although B 5 both in vegetation and fauna is somewhat intermediate to vegetation type 2 and fauna type IV (exposed hillsides, dry moss). B 5 is the only sample in this group with appreciable numbers of *Zercon curiosus*. The single fauna type V appears to extend into vegetation types 1, 4, 9 and 10, and a further type, not recognized by Russell & Wellington, represented by sample N 5. Fauna type IV is approximately equivalent to vegetation type 2 (exposed hillsides, dry moss) including samples of the L and K series. The sample S 9 is unique and represents fauna type I*a*, vegetation type 7 (sandy beaches). The samples H 1, H 2 and

* The first-built war-time hut referred to by Elbo (1953).

N 3 representing fauna type III are the only examples of vegetation type 8 (edges of streams and pools), although N 3 is invaded by animals from the adjacent vegetation type 9 (*Sibbaldia* banks). The series of samples Q 1–6 forming fauna type VII belong to vegetation type 23 (bare mountain tops). Fauna type I*b* is not represented in the vegetation analysis, being really a marine locality.

The rather remarkably good 'fit' between these two classifications, the one made by a botanically trained ecologist and the other by a zoologically trained ecologist and on separate occasions 10 years apart, would appear to indicate that their respective methods of classification do, in fact, describe a set of phenomena which have objective reality and that the fauna and flora are quite intimately related. The greater discrimination between the 'advanced' localities shown by the plants than by animals may possibly indicate that a sufficiently diverse fauna either has not yet reached the island or is not able to subsist there owing to other factors, such as the overwintering problem; it is very remarkable that a fauna almost as rich in species occurs in all the localities grouped under fauna V, and that, as discussed on p. 178, the fauna IV includes many of the same species in a more sparse distribution. This question is treated further in the concluding section.

The indices of moisture were very approximate, and it is hardly surprising that the relationships between these factors and the fauna are not very distinct. Fauna types I*a*, I*b*, and VII are evidently dry places according to both indices. Fauna III certainly occurs on wet places, and fauna II localities, where Collembola and Nematoda are most abundant are wet on the 'subjective moisture' scale. On the 'measured moisture' scale, indicating, it will be remembered, water-retaining capacity, these are often fairly dry. Fauna V, on the other hand, is mainly dry on the subjective and wet on the measured scale, indicating a porous soil, presumably rich in humus but a lower precipitation/drainage status. Fauna V is that in which the Oribatei attain their greatest development and these are widely regarded by other authors as being typical of drier localities (Hammer 1944, Strenzke in press). There is a fairly distinct gradient through the fauna IV samples on the subjective scale from drier to wetter following the change of the fauna from that resembling fauna V to that resembling fauna II. The measured scale is generally in the reverse direction indicating decrease in humus towards the fauna II end.

High plant matter content is confined to fauna V and, to a less extent, to some fauna III and IV sites. The localities of fauna I*a*, I*b*, and VII, on the other hand, are conspicuous for their poverty in combustible organic matter, as are the localities from which no fauna was extracted. No data are available for the fauna II localities which probably have a high plant matter content.

Data on soil particle size were limited to less than half the samples. The presence of fine (no. 5) particles is confined to fauna types II, IV and V where the richest faunas occur (no data are available for fauna VI). The impoverished fauna type VII is associated with very coarse sand grains.

The richest faunas are in the sheltered situations as might be expected, types II and V as a whole being sheltered, and the more exposed sites in fauna IV being the poorest in numbers of individuals. Faunas I*a*, I*b* and VII are in exposed localities with an open vegetation.

Fouling is consistently present in faunas II and VI; in the first it is due to birds and in the second to man. It is absent from the rich Oribatid areas of fauna V.

Rather surprisingly there is a good deal of evidence that mere locality, in defiance of other physical and vegetational factors, has some influence on the fauna type. This must presumably be mainly due to the mobility of the animals and their tendency to stray in quite large numbers from their characteristic habitats. Thus species from adjacent localities occur in sample N3, the entire fauna of all The Pillar localities (B series) is very similar despite the fact that four of Russell's plant groups occur here, and there are rather great differences between the floristically similar localities at Fishburn Valley (N series) and Seven Hollanders Bay (S series).

(*b*) *The characteristics of the fauna types*

This classification was carried out solely on the basis of the Acari and Collembola, localities and species being re-arranged as in Table 2 until those with the closest affinities were together and divisions being drawn between the different groups according to the distribution of the differential species. Since previous data on the kind of locality inhabited by any particular fauna did not exist, an equitable distribution of samples between the different fauna types was not to be expected. Thus fauna I*a* is represented by a single sample and fauna II by fourteen samples. Further, owing to low figures, it is often difficult to know exactly how samples from poorly represented faunas should be treated. Thus there are affinities, between VII, I*a*, II and III, between VI and V and especially between IV and V. If more samples of the type of J3 and Q5 had been obtained it is possible that these would have been allocated to a separate fauna in view of the many unique species they contained (see pp. 279, 280). The sparsely represented faunas warrant special attention on another occasion.

The main test of the validity of the divisions made here will be whether they recur in other geographical areas and at later dates. Meanwhile, the extent of correspondence with the floristic types, with physical factors, and with the groupings made by other authors afford some support for the contention that they mirror natural phenomena. The main features of each of the fauna types are:

I*a*. The *Oppia neerlandica* community of the shore vegetation.

Represented by a single sample from *Halianthus peploides* tussocks this must obviously be regarded as tentative. In favour of its recognition are the unique records of *Nanorchestes amphibius* and *Oribatula tibialis* (larva only) and the constancy and unusual abundance of *Oppia neerlandica* and *Brachychthonius sellnicki*. On the other hand, the affinities to fauna II are many; the following are common to the two types and absent or uncommon elsewhere:

Oppia neerlandica
Brachychthonius sellnicki
Pygmephorus cultratus var. *minor*
Oudemansium domesticum
Gamasodes berlesei (only Q7 among fauna II)

Affinities with fauna VII are indicated by *Microtydeus subtilis* which seems to be associated with very coarse sand grains; fauna VII, on the other hand, is quite distinct from fauna II.

The vegetation of the site is unique; the marine influence is shared by Q7 in fauna II

and by the I *b* localities (to which, however, there is no faunistic affinity). The presence of coarse sand allies this sample to the fauna VII localities.

I *b*. The *Archisotoma besselsi* community of the barren sea shore.

This community is sharply distinct from the others despite the appearance of casual individuals of the differential species in fauna V. It is distinguished by the absence of phanerogams and the animals' food supply is presumably marine in origin. Many specimens of *Bdella* species occur in this locality, but they were not extracted by the funnels owing to their low density; they are, however, very conspicuous and have been recorded by earlier authors.

II. The *Xenylla humicola–Onychiurus debilis* community of bird cliffs.

The main faunistic feature of these localities is the predominance of Collembola, usually with *Xenylla* constant and dominant, but in three cases with this species absent or casual and *Onychiurus duplopunctatus* instead. The only other species confined to this series of samples are not present in all of them, while those which are nearly constant occur as casuals elsewhere. *Penthaleus bipustulatus* and *Ameronothrus lineatus* are the mites which have the closest associations with this fauna, but, from their sporadic appearance elsewhere it would appear that some feature, perhaps moisture, is operating rather than bird fouling. There is some indication of a subdivision of the type II fauna following that of the differential species, and a further subdivision into those samples (Q 7, B 1, 2, 3, 4, 9 and 10) containing *Onychiurus macfadyeni*, *Oudemansium domesticum*, *Tullbergia krausbaueri* and *Folsomia bisetosa*, which are rather damper, and the better drained and perhaps less fouled samples which lack these species. But it is impossible to draw really firm distinctions. The flora and physical properties such as exposure vary considerably, but the main factors uniting this range of samples appear to be the fouling influence and rather damp conditions. The salt-water influence in Q 7 is reflected in the presence of two species otherwise confined to fauna I *a*.

III. The *Onychiurus groenlandicus* community of wet moss, without fouling.

This is represented by but two localities, one of which, N 3, lies within a few feet of the very richest type V locality (N 2) and therefore contains some accidental species from that area. The differential species occurs also in two damp moss localities in type II (B 7 and B 8) which are, to this extent, intermediate. This poorly represented type is tentative and can only be upheld by further investigation.

IV. The *Zercon curiosus* community of fjaeldmark and similar areas.

This is a somewhat unsatisfactory series of more or less impoverished samples, most of which share species with the type V fauna and a few with the type II fauna. There is a gradual change from samples approximating to the two types, accompanied by a change in moisture status as discussed in the first part of this section. Samples such as K 2 contain oribatids otherwise confined to fauna V, while the moister samples contain *Folsomia sexoculata* and *Brachychthonius sellnicki*. The high incidence of Trombidiformes is rather characteristic of this fauna, which would no doubt include at least two fauna types if larger samples were taken and a technique more suitable for the extraction of Trombidiformes were used.

V. The *Oribatula crassipes* community of dry phanerogam-dominated areas.

This group of localities has a very distinct fauna with many oribatid species, rather few collembola and the characteristic combination of a dry phanerogam flora, reaching its peak in the *Sibbaldia* banks, with shelter, and a humus-rich soil containing a high proportion of fine mineral particles. In addition to the chosen differential species, which has casual individuals in two type IV localities, *Oppia ornata*, *Trichoribates trimaculatus* and *Eobrachychthonius grandis* are almost equally characteristic of the fauna, and a total of twenty oribatids are confined to the fauna.

Two localities, S 5 and S 6, are marginal in that the fauna is here much poorer; however, species not found in other faunas but belonging to fauna V do occur in them. S 1 is marginal in that it has one unique species and two species found only in other fauna types. As mentioned at the beginning of this section this single fauna type covers five distinct plant types.

VI. The *Pygmephorus spinosus* community of the grassy patches indicating human habitation.

This highly peculiar combination of two species of *Pygmephorus* and the almost equally limited *Parasitellus ferox* is limited to the grassy patches near recent encampments. *Anurida remyi* and *Coelognathus putrescentiae* are limited to only one of these sites. The grass is a species not found elsewhere (although other grasses occur on Jan Mayen, of course) and the most important factor is probably human rubbish or excrement. *Parasitellus ferox* is characteristic of the European cave fauna when much rubbish is present (Turk, *in lit.*)

VII. *Microtydeus subtilis* community of exposed barren places.

These localities, in coarse barren stony areas, were not expected to yield a fauna. That *M. subtilis* is not confined to barren areas is indicated by its greater abundance in fauna I *a*, but it is one of the few species capable of surviving the unpromising combination of coarse sand, extreme exposure and lack of humus. *Folsomia sexoculata* and *Ameronothrus lineatus* were also found in these samples. Wilson (1948) showed that areas of bare sand on the island usually had a relatively rich flora of diatoms and these may provide food for the *Microtydeus subtilis*. Alternatively, other factors discussed below in connexion with locality Q 5 may have been operating to a lesser extent in the other examples of this fauna type.

Two samples showed a highly peculiar fauna worthy of note especially in connexion with future work of this sort.

J 3. This locality contained the following species not found elsewhere on the island:

Bdella longicornis var. *decipiens*
Microtydeus sp. near *rectangulus**
Brachytydeus sp. near *olivaceus**
Petralychus sp.*

It was also one of the sites of *Coccorhagidia* sp.* and one of the richest localities of fauna IV. The samples were taken among lichen-covered boulders at the foot of screes; the neighbouring samples, J 1 and J 2, were in lichen and in detritus between the boulders respectively, and they also yielded a fairly rich fauna including *Oppia ornata* and *Oribatula crassipes*. J 3 was in *Rhacomitrium* moss in the centre of lichen mats, presumably where, perhaps in accordance with a replacement cycle such as is

* These are considered by Dr F. A. Turk to be new species.

described by Watt (1947), the lichen has decayed and been replaced by moss. Possibly this special fauna is associated with a rather temporary phase of such a cycle, a hypothesis which suggests that it would be well worth while to take samples in close correlation with botanical replacement cycles in unstable soils such as are described by Wilson (1952). This would imply that the fauna is sufficiently well distributed to be able to exploit short-lived phases of the plant succession.

Q5. Despite the unpromising appearance of this locality the high spider and Collembola count obtained by field observation prompted sampling here. In addition to the species found in the other fauna VII localities the following were found in Q5:

Rhagidia sp.*	*Tydeus kochi*
Cyta latirostris	*Tectocepheus velatus*

The first three occur elsewhere only in fauna VII, and the last is confined to this fauna and other rather rich places. The samples were taken in a peculiar flaky brown volcanic rock where the spiders lived. The Collembola may well serve as food for the spiders, but the food of the former is uncertain. Either there is a locally rich algal flora and the fauna present is a self-supporting community or else this particular locality is one where, owing perhaps to some topographical feature, detritus is carried by wind currents or collected on snow and concentrated by runnels as the snow melts and tends to collect. The soil fauna may then be carried there from places where it is rich and be purely ephemeral or it may be permanently exploiting what appears to be a rather precarious food supply.

(*c*) *Comparison of fauna types with those recognized by other authors*

Hammer (1944) recognized three main soil fauna types in East Greenland:

The Platynothrus peltifer *community of lake banks etc.* Possibly owing to the very different geological formation of Jan Mayen with virtually no inland lakes, this association of animals appears to be completely lacking. Only a few of Hammer's 'occasional' species are found.

Oppia neerlandica	*Isotoma viridis*
Xenylla humicola	*Sminthurinus concolor*
Camisia horrida	

These seem to be associated with the less fouled sources of fauna II and the damper and richer fauna IV sites; perhaps the L series of samples are closest to this fauna.

The Oribatula exilis *community of* Salix herbacea *vegetation. Oribatula exilis* Nic. var. *crassipes* L. Koch appears to be the same as *O. crassipes* and also to be very similar to *O. tibialis* (Hammer 1944, p. 43). Ecologically speaking this community appears to be the same as the fauna V of Jan Mayen; other species common to the two are:

Calyptozetes sarekensis	*O. translameslata*
Oppia quadricarinata	*O. ornata*

and many floristic and physical features are the same. *Willemia anophthalma* was found in Greenland in this community but not on Jan Mayen, while a number of the Jan Mayen species are not recorded from East Greenland.

Ameronothrus lineatus–Archisotoma besselsi *community of beaches*. These two species were never found together on Jan Mayen and appear to inhabit quite distinct

* Considered by Dr F. A. Turk to be a new speciea.

areas; Hammer quotes many cases where they are not found together and the occasions when they are in the literature appear to be very few. On Jan Mayen *Archisotoma besselsi* seems to be almost confined to areas with a saline influence and *Ameronothrus lineatus* is only really abundant in the bird-fouled areas.

Strenzke (in press), describing a much less complete material from West Greenland (not of his own collecting), confirms Hammer's conclusions on the whole and adds *Tectocepheus velatus* to the *Oribatula exilis* community. On Jan Mayen this species certainly reaches its greatest abundance in these localities, but it is also very widespread elsewhere.

THE GENERAL DISTRIBUTION OF THE SOIL ANIMALS

The fauna of the localities described is most easily comprehended with the aid of two tables (Tables 1 and 2). The first of these gives the list of localities vertically, grouped according to the faunistic 'communities' derived in the last section and showing the numerical indices for the various habitat features as well as the occurrence of those members of the fauna which are not Collembola nor Acari. The faunistic 'communities' are solely derived from a consideration of the 'differential' Acari and Collembola so that coincidences with the habitat features and with the other members of the fauna are independent demonstrations of affinity.

The notes on the main species which follow are supplementary to Table 2, and should be read in conjunction with it; the numbers in the left-hand column of the table are intended to assist this process and all Collembola have been marked with an asterisk for the same reason. Table 2 does not cover all the sampling performed on the island; apart from the special studies concerned with changes in time of the fauna of locality B 2 reported in the next section and other special samplings, twelve localities are omitted because the fauna was extremely sparse or absent (these are the last twelve localities of Table 1). Also excluded are the eighteen species of Trombidiformes and three species of Oribatei listed in this section at the ends of the appropriate lists. These were represented only by isolated finds.

It is important to remember that, since the extraction efficiency of the apparatus varies from one type of animal to another, comparisons within the same column of Table 2 have little numerical validity, especially when made between the four separate taxonomic groups. Comparisons along a single row, however, can be made with more confidence. In the following notes figures in square brackets refer to the species order in Table 2.

Parasitiformes

This group, generally considered to be carnivorous (but this may not apply to *Dinychus* and *Trachytes*), conforms fairly well to the faunistic grouping based on the Collembola and other mite suborders. Owing to the larger size and lower densities of these forms, rather small numbers were taken in any one sample and this may partly account for their rather sporadic appearance within the faunistic types. It is noteworthy that the four species of the genus *Zercon* appear to have recognizably different ecological requirements.

Veigaia kochi (Träg. 1901) [51]. Mainly in fauna V, all sites are sheltered, south-facing and with a dry higher plant flora.

Pergamasus sp. [9]. A single protonymph. Site combining sea-water influence with fouling from kittiwake colony.

Parasitellus ferox (Träg. 1910) [84]. In B 11 and S 7, *Zercon franzi* is abundant, otherwise this species is confined to habitats which are marginal for other parasitid species. In Europe this is a cave-dwelling species.

Gamasodes berlesei Willm. 1935 [1]. The distribution of this species cuts across the fauna classification because locality Q 7 is both a bird cliff and a sea-shore site. The features of salt-water influence, coarse sand particles and decay in organic matter are common to both localities, but the remainder of the fauna is very different.

Zercon curiosus (Träg. 1910) [32]. This species is present in a much wider variety of samples than any other parasitid. As explained in the discussion on faunistic type IV (p. 278) this can be regarded as a fairly typical member of this fauna. The distribution follows closely that of *Brachychthonius scalaris* and of *Nanorchestes arboriger* but all three are widespread species. In general this species appears to occur in localities which are too sparsely vegetated or with too impoverished a fauna for the other *Zercon* species and to avoid those places where the other species are abundant; however it is restricted to areas with numerous Collembola.

Zercon perforatulus Berl. [56]. Constant and quite abundant in a single locality with a very rich Oribatid fauna and unusually high plant matter content in the soil.

Zercon franzi Willm. [24]. This is constant in the majority of the fauna II localities but also in N 2, S 7, S 8 in fauna V and VI. The main features shared by all these samples are the dense turf-like structure of the vegetation, the high ratio of plant matter and the high proportion of finer mineral particles in the soil. This is the species of parasitid found in the highest densities, and is to some extent mutually exclusive with *Z. inornatus*.

Zercon inornatus Willm. [8]. Only constant in B 10. All sites have saxifrages present, often with other higher plants. In all *Folsomia sexoculata* is abundant and constant. Not found in the dry sites among fauna V.

Trachytes infirmus Berl. 1887 [55]. The only example of Russell & Wellington's (1940) vegetation type 4 and one source of *Myzodium rabeleri* (Aphidae). This locality had an unusually diverse Oribatid fauna.

Dinychus perforatus Kram. (syn. *Phyllodinychus tetraphyllus* (Berl.))* [10]. One of the few examples of Russell & Wellington's vegetation type 2, and the other source of a *Myzodium rabeleri* (Aphidae). A single specimen only.

Additional species are: *Parasitus kempersi* Ouds. [5], *Cyrtolaelaps mucronatus* G. & R. Can. (syn. *brevispinosus* (Träg.)) [7].

Trombidiformes

The sixty species of mites belonging to this group usually occur in very low densities in a rather sporadic manner; it is difficult therefore to classify them satisfactorily in the fauna types. They are a group of small mites of diverse habits and little is known of their ecology. Some genera such as *Rhagidia* are generally believed to be carnivores (remains of *Xenylla humicola* were found and in several *Rhagidia gelida* by the author). Others such as *Bryobia* and the Tydaeidae are known to be herbivores and are evidently

* Dr F. A. Turk regards this as probably a new subspecies.

closely tied to the distribution of certain plants (*Tydeus totensis* and *T. svalbardensis* are always associated with mosses). The presumably carnivorous *Pygmephorus* species are almost entirely restricted to grass areas and two are indicator species for type VI fauna of the grass patches of Jøssingdalen (V series).

Variatipes tridentinus Paoli 1911 [94]. All localities (except J3, see p. 279) with higher plants and closed vegetation, fairly sheltered and with a numerous arthropod fauna.

Pygmephorus cultratus Berl. 1904 [33]. Dampish, sheltered, closed vegetation.

Pygmephorus cultratus var. *minor* Berl. 1904 [17]. All samples share fouling with presence of higher plants, and dampness.

Pygmephorus stercoricola Berl. 1904 [58]. (Present N1, casual S2). Strictly limited to the *Sibbaldia* banks, Russell & Wellington's (1940) type 9, the richest vegetation of all with the best developed humus.

Pygmephorus tarsalis Hirst 1921 [83]. Constant, abundant, differential species for type VI, a single casual also in B3, which is similar in having some fouling, and being protected but which has *Oxyria digyna*, merging into grasses.

Pygmephorus spinosus Kram. 1877 [82]. Constant, abundant differential species for fauna type VI, Russell & Wellington's (1940) vegetation type 22.

Eupodes variegatus Koch 1838 [92]. Casual in ten different localities, all with vegetation.

Cocceupodes molicellus (Koch 1838) [42]. Constant only in type V fauna but occurs in twelve other localities with some shelter and a closed vegetation.

Cocceupodes curviclava Thor 1934 [87]. All these localities except J3 and Q5 (see pp. 279, 280) have higher plants, and all are areas of a moderately dense animal population.

Halotydeus destructor Jack. An individual of this pest of potatoes found in L3 in Jøssingdalen may have been introduced with food by troops during the war.

Protereunetes börneri Thor 1934 [93]. All localities somewhat sheltered, with fine soil particles and moderate or high plant matter content.

Protereunetes börneri Thor 1934 subsp.* [36]. Drier exposed places with open vegetation and *Salix herbacea* or moss. Scott Russell's vegetation type 5.

Protereunetes brevipes (Berl. 1923) [96]. All sites sheltered without low plant-matter content and with closed vegetation.

Penthaleus bipustulatus (Herm. 1904) [18]. All localities are dampish and have vegetation, the more typical drier type V areas being avoided.

Penthalodes ovalis (Duges 1834) [21]. All localities are damp and protected with a closed vegetation, mosses and not less than 7% plant matter.

Cyta latirostris (Herm 1804) [49]. Casual only in seven samples all sheltered, with flowering plants (except Q5, see p. 280). Perhaps preferring drier localities than *Bdellodes longirostris*.

Bdella longicornis (Linn 1758) (syn. *Bellidium vulgaris* (Herm)) [57]. (Present S8, casual N1, N5, N6, S2.) Limited to areas with dicotyledons and not less than 14% plant matter in fauna V.

* Dr F. A. Turk regards this as a new subspecies.

Bdellodes longirostris (Herm 1904) [11]. Restricted to fauna II. Note the division of habitats between the four species of Bdellidae.

Neomolgus littoralis (Linn). Not found by soil sampling, but taken from rocks in Tornoe delta by sweeping.

Rhagidia gelida Thorell 1871 [27]. Mostly damper places, including sea-shore; avoids the area of fauna V, where *R. terricola* occurs.

Rhagidia birulai Thor 1909 subsp.* [90]. Dry areas with higher plants, and *Brachychthonius scalaris* present.

Rhagidia terricola (Koch 1836) [46]. Widespread in type V and in type IV localities with drier vegetation, fine soil particles and moderate plant matter (Russell & Wellington's (1940) type 5). This species seems to be complementary in its distribution to *R. gelida*.

Rhagidia sp. [88]. This undescribed species occurs in the few localities with coarse mineral particles dominating (see p. 280 with reference to Q5).

Coccorhagidia clavifrons (R. Can. 1886) [61]. Dry protected areas with *Salix herbacea*.

Coccorhagidia sp. [47]. An undescribed species constant in S3 and casual in seven other localities in types IV and V. The less rich localities in type V and those in type IV with small soil particles and a richer fauna.

Ereynetes sp. [91]. An undescribed species near *sittardensis* casual in four very various localities.

Tydeus interruptus Thor 1932 [45]. Confined to dry places with a fairly rich fauna and some humus.

Tydeus svalbardensis Thor [19]. Rather erratic distribution, confined to damper places, closed vegetation always containing mosses.

Tydeus totensis Thor 1932 [35]. Drier slopes always with a closed vegetation including mosses and 7–60% plant matter. Fouling appears to be irrelevant.

Microtydeus similis Can. 1886 [43]. Widely dispersed, mainly confined to areas of closed moss vegetation with intermediate values of plant matter, some shelter and always a preponderance of fine soil particles.

Microtydeus constans Thor 1931 [44]. Sporadic in south-facing areas with higher plants and fine soil particles.

Microtydeus subtilis (Koch 1838) [86]. Constant and abundant Q4, Q5, S9, and regarded as the differential species of fauna types I*a* and VII. These correspond to Russell & Wellington's (1940) vegetation types 7 and 23, and the localities share extreme exposure, open vegetation with a preponderance of large soil particles and not more than 2% plant matter in the soil. It was not expected that these very barren places would have any soil fauna at all.

Coccotydeus frequens Grandjean 1939 [38]. Casual only. Open or closed vegetation with moss and *Salix* or flowering plants. Not less than 7% plant matter.

Nanorchestes arboriger Berl 1905 [37]. Extremely widespread, but constant in a higher proportion of type IV localities than the others. With regard to Russell & Wellington's (1940) flora types, only type 7 is avoided and this species is constant in all localities of types 1, 2, 4, and some of 10, 15, 17, 20 and 23. Absent from areas of very

* Dr F. A. Turk regards this as a new subspecies.

sparse vegetation and very wet places. This mite probably lives mainly in the vegetation and not the soil, which may account for its sporadic occurrence in the samples.

Speleorchestes sp. An undescribed species found in Jøssingdalen in a locality like L3, but not one of the normal soil samples.

Bryobia graminium (Schrank 1787) [20]. Areas with a relatively dry closed vegetation with 7–60% plant matter.

The distribution of the following sparse species will be apparent from Table 2 and calls for no comment:

Tarsonemoides uliginosus Willm. [31]
Coccotydeus tenuiclaviger Thor. [89]
Alicorhagia plumipilus Thor. [95]
Alicorhagia clavipilus Thor. [59]
Petrobia latens (O. F. Müll.) [60]

The following, represented by only casual records, have not been included in Table 2; the samples in which they were found are indicated in parentheses:

Scutacarus crassisetus var. *pannonicus* Willm. (V4)
Pygmephorus inconspicuus Berl. (B4)
Eupodes viridis Ouds. (E1)
Cocceupodes paradoxus Weis-Fogh. (E1)
Penthaleus major (Duges) (Q7)
Bdella longicornis var. *decipiens* Thorell (J3)
Rhagidia reflexa (Koch) (K3)
Opsereynetes norvegicus Thor. (N2, N5)
Tydeus kochi Ouds. (N1, Q5)
Tydeus tridactylus Weis-Fogh. (B3, B4, B5)
Tydeus sp. (larva only) (K3)
Tydeus sp. (near *subterraneus*) (E1)
Microtydeus sp. (near *rectangulus*) (J3)
Brachytydeus sp. (near *olivaceus*) (J3)
Alicorhagia fragilis Berl. (B4)
Nanorchestes amphibius Top. Trouess. (S9)
Bryobia praetiosa Koch (S7)
Petralychus sp. (J3)

Cryptostigmata: Acaridiae

These are forms found frequently in connexion with human habitation, and since it was not possible under expedition conditions to ensure absolute sterility some of these animals might have entered the samples after sampling occurred. However, the constancy and high numbers of *Oudemansium* in the B series of samples where bird fouling was present point to this animal having truly come from there. The remaining species occur in few samples only.

Oudemansium domesticum (Degeer 1771) [28] is only abundant and constant in the B series (fauna type II), but casual animals occur in samples from all but the very damp places. This species is believed to feed on coprophilous fungi (Turk, *in lit.*).

Histiostoma sp. [75]. Casual in N2 and N4, the damper samples of fauna type V, with a well-developed vegetation (Russell & Wellington's (1940) type 9).

Kosmoglyphus krameri Bul. 1881 [76]. Constant in S3 only. Dry, sheltered well-developed vegetation, Russell & Wellington's (1940) type 10.

Tyroborus lini Ouds. 1924 [97]. Both places have grass in a rich vegetation.

Coelognathus putrescentiae (Schrank 1781) [85]. Dry sheltered valley bottoms with closed vegetation including grass and high proportion of plant matter in the soil.

Cryptostigmata: Oribatei

The Oribatei show their greatest development in the type V fauna and only two species are restricted to any of the other faunas, while twelve are completely restricted to the type V fauna. This occurs where the greatest development of a phanerogamic

flora takes place, namely the localities which are well sheltered, south-facing and which receive mineral nutrients from the underlying basaltic rocks. The peak of such floristic types is the *Sibbaldia* banks (Russell & Wellington's (1940) type 9), but in fact the Oribatid fauna seems to be most numerous and to have most species in Russell & Wellington's type 10 localities (consolidated hollows in lava fields): the fauna is essentially the same in both, however, and it is not easy to distinguish between them.

It has unfortunately not been possible to obtain a unanimous decision at present about the identity of some of the Oribatid species. The names given in this paper are those due to Dr F. A. Turk, but partly owing to recent advances in taxonomy of arctic Oribatids and partly owing to different interpretations of the names used by earlier workers, the following species may not be correctly named: it is intended that this matter will be cleared up in Dr Turk's paper on taxonomy which is due to be published shortly.

Brachychthonius scalaris and *B. sellnicki*. There may be some confusion between these species and one or more other species may be included among the latter, which may be identical with *B. lapponicus*.

Oribatula crassipes and *O. tibialis*. Dr Strenzke is of the opinion that these two species are identical, while Dr Forsslund believes them to be different, and that the usage adopted here is correct.

Ceratoppia bipilis may be *C. hoeli*.

Trichoribates trimaculatus may be *Diapterobates notatus*.

The genus *Nothrus* is at present undergoing revision by Dr van der Hammen and the present nomenclature may require alteration.

Brachychthonius scalaris (Forsslund 1942) [98]. Constant in twenty-eight localities covering all fauna types except I and III. This species appears to avoid the very damp areas and those with a very low content of organic matter; it is most abundant where higher plants and other Oribatids occur. It is to some extent complementary to *Br. sellnicki*.

Brachychthonius sellnicki Thor. [3]. Constant in five localities in fauna type II, also in one each of types IV and VII. This species only seems to occur outside type II fauna in damp localities. It is confined to areas of closed vegetation, having only 1–7% plant matter in the soil. The distribution is the same as that of the bacteria-feeding Nematoda. Hammer (1946) states that this species prefers luxuriant moss localities.

Brachychthonius horridus Sellnick 1926 [40]. The type IV localities are all ones with 20% or more plant matter and none have very coarse soil particles.

Brachychthonius sp. [74]. A single individual of an undescribed species from S1, a unique locality.

Brachychthonius berlesei Willm 1928 [63]. The two constant localities both belong to Russell & Wellington's (1940) type 9 and both have *Salix herbacea* but have higher plant matter content and a richer fauna than other *Salix* areas outside Fishburn Valley. Note that this species and *Eobrachychthonius grandis* are mutually exclusive, within the type V fauna.

Eobrachychthonius grandis Sellnick 1944 = *E. sexnotatus* Jacot (see Strenzke, in press and Forsslund, personal communication.) [73]. This geographically widespread species covers a much wider range within the type V localities than *E. berlesei* being constant in five out of the eleven; none of the five contain *Salix herbacea*.

Camisia horrida var. *borealis* (Thorell) Träg. 1904 [39]. Limited to the drier fauna IV areas with moss or *Salix herbacea* forming closed vegetation. The more exposed places are avoided. Hammer (1946) states that it has a preference for drier localities.

Nothrus borussicus Selln. 1926 [71]. All localities with higher plants.

Heminothrus paolianus Berl. 1921 [67]. All sites have a dense cover of higher plants and a high content of plant matter.

Hermannia reticulata Thorell 1871 [100]. Although constant in some marginal fauna V localities this is not a typical member of that fauna, being constant also in B 11 (fauna II) and present in other localities of faunas II, III and IV. The only common factors are a closed vegetation with moss usually present, and fine soil particles. Both Hammer (1944) and Strenzke (in press) regard this as an inhabitant of drier places; this appears to be only broadly true of the Jan Mayen distribution, and of Hammer's (1952) specimens from arctic Canada.

Damaeus ursina [72]. Apparently limited to the Fishburn Valley and to areas with higher plants.

Metabelba sp. (undescribed) [48]. All localities are dominated by lichens and with more than 20% plant matter; note that this distribution contrasts strongly with that of the other Belbidae.

Belba compta (Kulcz 1902) [77]. This is absent from places with lichens (cf. *Metabelba*) and in general seems to occur in the very richest plant types within type V (cf. *Damaeus ursina*). The two species occurred together only in N 1.

Ceratoppia sphaerica (L. Koch 1838) [101]. Casual in seven localities in fauna types II, IV, V. These show a wide range of vegetation and all other factors considered, but all have a moderate or high water content, closed vegetation usually including moss and moderate shelter. The more extreme types are avoided.

Oppia neerlandica sensu Willman 1931 (*O. corrugata* Berl.) vide Strenzke (in press) [2]. This species occurs in three of the fauna II sites but is most abundant and is constant in S 9, the one type I *a* site. All four sites have an open vegetation of flowering plants, decaying animal matter, and plant matter contents below 8%. Strenzke quotes this species as an inhabitant of salt-containing sea-shore soils of north Germany, but Hammer (1946, 1952) states that it occurs in a wide variety of conditions in Greenland and arctic Canada.

Oppia maritima Willm. 1929 [66]. Limited to S 7, where it is constant. Hammer (1944) also found that this is not confined to sea coasts, being characteristic of her 'dry biotopes, *Cassiope* heath and fell field'. S 7 is perhaps the closest approach to this type on Jan Mayen.

Oppia ornata (Ouds 1900) [53]. This species is characteristic of type V but also has casual specimens in J 1 and J 2 (type IV). The type V localities from which they are absent are S 1, S 5 and S 6 which are very 'dilute' localities dominated by lichens or with bare gravel. Absent from the *Empetrum* locality N 5. This agrees with Hammer

(1946) and Strenzke (in press) who finds this species in drier localities especially with moss.

Oppia translamellata (Willm. 1923) [68]. All sites have a continuous carpet of *Salix herbacea* or *Vaccinium*. Regarded as an inhabitant of wet places by Hammer (1946, 1952) and Strenzke (in press), but drier places on Jan Mayen are wet by comparison with European standards.

Oppia quadricarinata (Mich. 1888) [70]. Hammer (1946) states that this species has 'a decided predilection for dry localities'. This is true on Jan Mayen also.

Suctobelba trigona (Mich. 1888) [69]. Confined to fauna V.

Suctobelba sp. [50]. Sites in well-drained valley bottoms with moss or lichen. These have a much less rich fauna than the localities of *Suctobelba trigona*.

Tectocepheus velatus (Mich.) [99]. This wide-ranging species occurs in all fauna types but I and VI; it is only constant however in V and one site in IV, all of which are sheltered sites. Fully exposed localities and those with extremes of fouling or sea-water influence are avoided and areas of drier vegetation preferred. Both Strenzke (in press) and Hammer (1946, 1952) remark on the widespread distribution of this species, while Turk (*in lit.*) confirms that in Cornwall it is limited to most sheltered localities.

Ameronothrus lineatus (Thorell) [29]. Constant in fauna type II only; Russell & Wellington's (1940) types 19 and 20. However, casual individuals occur in eleven other localities in all fauna types except type I. Strenzke (in press) states that this species is restricted to areas influenced by sea water in North Germany, but not in West Greenland, and that it is 'ornithokoprophil' in Spitsbergen. This is supported by the Jan Mayen distribution. Hammer (1944) found it in 'clayey beach meadows submerged during high tide'.

Ameronothrus nigrofemoratus (L. Koch) [12]. Closed vegetation with bird fouling, damp and sheltered. Hammer (1946) and Strenzke (in press) stress this species' ability to withstand prolonged flooding.

Oribatula crassipes (L. Koch) [54]. This species has also an isolated casual individual in N 3, the wetter locality of type III: resembles *Oppia ornata* in that its range includes some type IV as well as type V localities.

Liebstadia similis (Mich.) [52]. A most erratic distribution; only E 6 lacks a definite humus. Hammer indicates a preference in Greenland for grassy slopes but in Germany (Strenzke, in press) this species prefers wet and brackish places and Hammer (1952) finds it in wet depressions in arctic Canada. None of these descriptions fit the limited Jan Mayen distribution exactly.

Trichoribates trimaculatus (Koch) [64]. This is probably the best differential species for the type V fauna, being constant in six, present in three, casual in one and absent from only two of the localities; these two, S 1 and S 5, are very 'dilute' versions of type V, being dominated by dry lichens. This distribution is followed almost exactly by *Oribatula crassipes*, which, however, has casual specimens in types III and IV.

Calyptozetes sarekensis (Trägårdh) [62]. Hammer (1937, 1944, 1946, 1952) believes this species to feed on lichens. These were reported from all Jan Mayen localities except N 2. They were not listed from here by Russell & Wellington (1940, p. 174) but they could have been overlooked in so dense a flora.

Pelops approximatus Hull. [65]. In all localities moss is present as well as higher plants and the soil has a high water-holding capacity and not less than 60% plant matter.

The following are represented by isolated individuals, and are not included in Table 2:

Oribatula tibialis? (Nic.) (larva only, S 9)
Nothrus sylvestris Koch 1836 (1 individual N 2; an unexpected find)
Carabodes labyrinthicus (Q 7)

Collembola

Eight of the twenty-one species of Collembola are characteristic of fauna II and none are confined to any other fauna type; the vast majority of individuals (over 6000) occur here. It would be wrong, however, to attribute this solely to the bird-fouling influence, because few are confined to places where fouling occurs. It seems probable that the higher water content of these soils is another factor attracting the Collembola and that their absence from fauna V is mainly due to this area being drier. Within fauna II there is a fairly clear distinction into a number of subtypes with different dominant species, e.g. *Onychiurus duplopunctatus* and *Xenylla humicola* are almost mutually exclusive; however this is not regarded as justification for dividing this fauna type in two (see Braun-Blanquet 1932). There can be no doubt that the Collembola do not conform as closely to the faunistic groupings as the mites. This is also mentioned by Hammer who suggests that 'this is due to the high ecological valence of Greenland collemboles'.

Hypogastrura succinea Gisin 1949 [13]. Confined to damp fouled sites at the foot of bird cliffs, all sheltered and with closed vegetation. All are sites where both *Xenylla humicola* and *Folsomia sexoculata* are constant and abundant.

Xenylla humicola (Fab.) Tulb. [22]. This species is constant and abundant in all the type II*a* fauna sites but is absent from two and only 'present' in one of the II*b* sites. It is only constant elsewhere in C 3 (type I*b*) and S 2 (type V). Casual individuals however extend the range to all other fauna types except VII, and all Russell & Wellington's (1940) vegetation types except 7 (sandy beaches). The only places from which *Xenylla humicola* is absent are those greatly lacking plant matter in the soil, the exposed places and the dry places which lack vegetation.

Willemia anophthalma, Börner [103]. Isolated individuals in K 3 and V 1, which sites have little in common other than being in the same valley and resembling the sites listed by Hammer (1938) who regards this as an inhabitant of dry biotopes (1944).

Micranurida pygmaea Börner [104]. Casuals in V 1, J 4 and K 4, which also have little in common except presence in the same valley.

Anurida remyi Denis 1948 [4]. Constant V 2 (type VI) present Q 7 (II) and casual in S 9 (VII). These localities have little in common except the presence of enchytraeids and some sort of decaying animal matter.

Onychiurus groenlandicus Tulb. [30]. This species occurs in the two sites which are very damp with running water but have no fouling; its low density in these places is believed to be due to the poverty of the sites, and its presence also in the damp, least fouled areas B 7 and B 8 within the type II fauna justifies the creation of a fauna type III

of which, it is thought *O. groenlandicus* would be the differential species if larger samples were taken. All these localities have a closed moss fauna and *Smittia* fly larvae present. Hammer (1938) regards it as preferring moist moss localities.

Onychiurus macfadyeni Gisin 1953 [106]. This species is absent from fauna type I*b* only and from Russell & Wellington's (1940) vegetation types 7, 14, 15. It is most abundant in sites with a high arthropod population and avoids areas with lichen only, moist, maritime and barren areas. It has been found since Gisin's paper by Dr K. Strenzke (personal communication) as a littoral species in north Germany.

Onychiurus duplopunctatus Moniez [15]. Dr Gisin and Dr Strenzke, to whom I am indebted for this information, have now decided that this species differs from *O. debilis* in having among other features two instead of one pair of pseudocellae on thorax segment I. The new description of the species, *O. duplopunctatus*, is to be published by Dr Strenzke. Within fauna type II this species might almost be regarded as the type of a subfauna characterized by its presence and that of enchytraeid worms, while *Xenylla humicola*, *Brachychthonius scalaris*, *Tectocepheus velatus* and other species are absent. Physically the sites are all small tussocks of moss or saxifrage anchored in crevices on the bare rock. D 1 differs from the rest in lacking any proven bird cliff influence (but see p. 273). For reasons already given the substitution of one dominant by another is not regarded as sufficient justification for erecting a separate fauna type. None of the localities containing this species have more than 7% plant residues.

Onychiurus arcticus (Tullb) [16]. This striking species was confined to the single locality B 11 which combines the presence of fouling with that of a higher plant in a cleft of the bare rock.

Tullbergia krausbaueri Börner [25]. Although constant in five type II sites and only one type V site, this species occurs in more sites in types V and IV than type II and generally prefers the drier areas and areas with a high density of arthropods throughout. Casuals occur also in types VI and VII. Hammer (1944) mentions that this is a species of dry areas.

Tullbergia arctica Wahlgren [14]. Damp sheltered sites with higher plants dominating and fouling, although often present, less pronounced than in the *Hypogastrura succinea* localities.

Pseudanurophorus binoculatus Kseneman [81]. Only a single casual individual outside fauna V, in K 2. All sites have *Salix herbacea* present, are dry and sheltered, with between 14 and 20% plant matter and coarser mineral particles dominating.

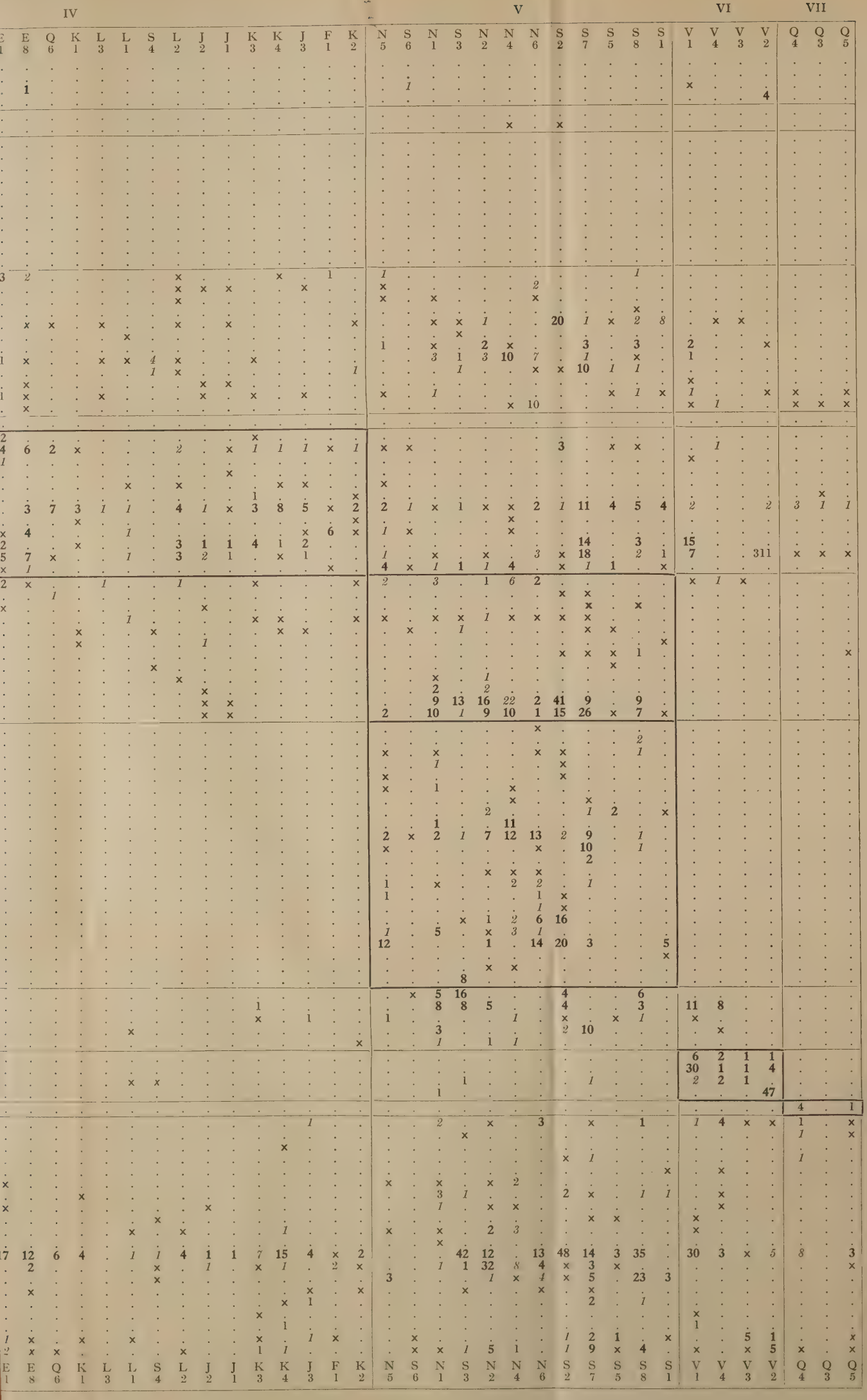
Folsomia sexoculata (Tullb) [41]. This species is constant in a number of localities in types II and IV as well as one each of III, IV and VI; the main characteristics of all these places seem to be the damp, closed vegetation; exposed places are however especially favoured. In view of the poverty of most of the damper sites of fauna IV, this species seems justifiably regarded as characteristic, in fact it is often the only species present. The distribution, which resembles that described by Hammer (1938), is partly complementary to that of *Xenylla humicola*, but there are sites in fauna II where both are constant and abundant.

Folsomia bisetosa Gisin 1953 [26]. This species has a distribution very similar to that of *Tullbergia krausbaueri*.

		Ia	Ib								II								III											
		S	C	C	C	B	B	B	B	Q	B	B	B	B	B	B	B	D	H	N	A	E	E	E	E	J	F	H
		9	1	2	3	8	5	13	7	7	9	3	10	4	2	1	11	12	1	1	3	3	2	4	6	4	4	2
1	*Gamasodes berlesei*	x	.	.	.	.	.	.	.	*5*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	*Oppia neerlandica*	**71**	.	.	.	.	.	.	.	.	.	.	1	.	**7**	*2*	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	*Brachychthonius sellnicki*	**24**	.	.	x	*1*	**10**	x	.	.	**1**	**5**	**9**	**2**	.	x	.	.	x	1	*2*	**3**	.	.	.	x	.	.	.	.
4	**Anurida remyi*	x	.	.	.	.	.	.	.	*1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5	*Parasitus kempersi*	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6	**Archisotoma besselsi*	.	**17**	*1*	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7	*Cyrtolaelaps mucronatus*	.	.	.	.	.	.	.	.	.	.	.	.	x	x	*3*	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8	*Zercon inornatus*	.	.	.	.	1	.	.	x	.	.	x	3	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
9	*Pergamasus* sp.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
10	*Dinychus perforatus*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
11	*Bdellodes longirostris*	.	.	.	.	.	.	.	.	.	x	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
12	*Ameronothrus nigrofemoratus*	.	.	.	.	.	.	.	.	.	.	**3**	x	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.
13	**Hypogastrura succinea*	.	.	.	.	.	.	.	**2**	**3**		**3**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
14	**Tullbergia arctica*	.	.	.	.	.	**6**	.	.	.	.	**8**	**1**	*3*	*3*	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
15	**Onychiurus duplopunctatus*	.	.	.	.	.	.	.	x	.	*4*	.	.	.	.	.	**25**	*15*	**6**	.	.	.	.	.	.	.	.	.	.	.
16	**O. arcticus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**2**	.	.	.	.	.	.	.	.	.	.	.	.	.
17	*Pygmephorus cultratus* var. *minor*	x	.	.	.	.	.	.	.	.	.	*1*	.	*1*	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18	*Penthaleus bipustulatus*	.	.	.	.	*1*	**1**	x	**2**	.	**6**	*1*	x	x	*1*	*2*	**1**	**2**	.	.	.	x	.	.	.	.	.	.	x	.
19	*Tydeus svalbardensis*	.	.	.	.	.	**4**	.	*3*	.	.	.	.	x	.	.	x	x	.	.	.	.	.	.	.	.	.	.	.	.
20	*Bryobia graminium*	.	.	.	.	.	**1**	.	.	.	.	.	.	*1*	*1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
21	*Penthalodes ovalis*	.	.	.	.	x	.	.	.	.	.	.	.	x	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.
22	**Xenylla humicola*	.	.	.	**3**	**11**	**9**	**75**	**28**	**141**	**32**	**61**	**39**	**46**	**55**	**42**	*x*	.	.	.	x	.	x	.	.	.	.	x	.
23	**Sminthurinus concolor*	.	.	.	.	x	x	*x*	*1*	.	*1*	x	x	x	.	1	x	.	.	.	.	.	.	.	.	.	.	.	.	.
24	*Zercon franzi*	.	.	.	.	x	**4**	.	*1*	**4**	*2*	**7**	.	*2*	**3**	**10**	**4**	.	.	.	x	.	.	.	.	.	.	.	.	.
25	**Tullbergia krausbaueri*	1	.	.	.	.	1	.	.	.	.	30	9	1	**4**	**28**	.	.	8	.	.	.	.	*3*	.	.	.	.	.	.
26	**Folsomia bisetosa*	.	.	.	.	.	*1*	.	.	.	.	95	.	**6**	**8**	.	**4**	x	.	.	.	.	.	.	.	.	.	.	.	.
27	*Rhagidia gelida*	.	x	.	.	x	.	.	x	.	*1*	.	*1*	.	*2*	.	.	.	.	.	.	x	.	.	.	.	x	.	.	.
28	*Oudemansium domesticum*	x	.	.	x	x	*1*	.	.	.	x	*20*	*2*	*8*	x	**176**	1	x	.	.	.	.	x	.	.	x	x	.	.	.
29	*Ameronothrus lineatus*	.	.	.	.	.	.	.	.	**9**	x	**4**	x	.	x	*1*	**19**	**20**	.	.	x	.	.	.	x	.	.	.	.	x
30	**Onychiurus groenlandicus*	.	.	.	.	*1*	.	.	*2*	.	.	.	1	.	.	.	.	.	.	x	1	.	.	.	.	.	.	.	.	.
31	*Tarsonemoides uliginosus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
32	*Zercon curiosus*	.	.	.	.	.	*1*	.	.	.	.	.	.	x	.	.	.	.	.	*1*	.	.	.	.	.	x	**2**	*1*	.
33	*Pygmephorus cultratus*	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.
34	*Protereunetes striatellus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.
35	*Tydeus totensis*	.	.	.	.	.	.	.	.	.	.	.	.	*1*	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
36	*Protereunetes börneri* subsp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
37	*Nanorchestes arboriger*	.	.	.	.	*1*	**4**	*1*	*2*	.	*1*	*2*	**3**	**4**	*3*	.	*x*	.	*1*	.	.	.	.	.	.	.	*1*	5	.	.
38	*Coccotydeus frequens*	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
39	*Camisia horrida* var. *borealis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	*1*	.	.	.	.
40	*Brachychthonius horridus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.
41	**Folsomia sexoculata*	.	.	.	.	*2*	.	*2*	**6**	**77**	**3**	**58**	**10**	.	x	.	**75**	*11*	**3**	*2*	**7**	**2**	*1*	*1*	**4**	**5**	*1*	**1**	*2*	
42	*Cocceupodes molicellus*	.	.	.	.	.	*1*	.	x	.	.	.	1	.	x	.	1	x	.	x	x	.	.	.	.	.	.	x	.	.
43	*Microtydeus similis*	.	.	.	.	x	.	.	.	.	.	.	1	*1*	x	.	x	.	.	.	x	.	.	.	.	.	x	.	.	.
44	*M. constans*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
45	*Tydeus interruptus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
46	*Rhagidia terricola*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
47	*Coccorhagidia* sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
48	*Metabelba* sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
49	*Cyta latirostris*	.	.	.	.	.	x	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
50	*Suctobelba* sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
51	*Veigaia kochi*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
52	*Liebstadia similis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.
53	*Oppia ornata*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
54	*Oribatula crassipes*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.
55	*Trachytes infirmus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
56	*Zercon perforatulus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
57	*Bdella longicornis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
58	*Pygmephorus stercoricola*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
59	*Alicorhagia clavipilus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
60	*Petrobia latens*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
61	*Coccorhagidia clavifrons*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
62	*Calyptozetes sarekensis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
63	*Brachychthonius berlesei*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
64	*Trichoribates trimaculatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
65	*Pelops approximatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
66	*Oppia maritima*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
67	*Heminothrus paolianus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
68	*Oppia translamellata*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
69	*Suctobelba trigona*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
70	*Oppia quadricarinata*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
71	*Nothrus borussicus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
72	*Damaeus ursina*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
73	*Eobrachychthonius grandis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
74	*Brachychthonius* sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
75	*Histiostoma* sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
76	*Kosmoglyphus krameri*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
77	*Belba compta*	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
78	**Isotoma notabilis*	.	.	.	.	.	.	.	.	.	.	.	.	*1*	.	*4*	.	.	.	.	.	.	.	.	.	x	.	.	.	.
79	**Neelus minimus*	.	.	.	.	.	x	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
80	**Isotomiella minor*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
81	**Pseudanurophorus binoculatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
82	*Pygmephorus spinosus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
83	*P. tarsalis*	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
84	*Parasitellus ferox*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*1*	x	.	.	.	.	.	.	.	.	.	.	.	.
85	*Coelognathus putrescentiae*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
86	*Microtydeus subtilis*	**11**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
87	*Cocceupodes curviclava*	.	.	.	.	.	x	*1*	.	.	2	.	.	.	*2*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.
88	*Rhagidia* sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
89	*Coccotydeus tenuiclaviger*	.	.	.	.	.	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
90	*Rhagidia birulai*	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
91	*Ereynetes* sp. (near *sittardensis*)	x	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
92	*Eupodes variegatus*	.	.	.	.	.	x	.	.	.	.	.	.	.	x	x	.	.	.	.	x	.	.	.	.	x	.	.	.	.
93	*Protereunetes börneri*	.	.	.	.	x	.	.	x	.	1	1	1	x	x	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.
94	*Variatipes tridentinus*	.	.	.	.	.	.	.	.	.	x	.	.	.	.	x	.	.	x	.	.	.	.	.	.	.	.	.	.	.
95	*Alicorhagia plumipilus*	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
96	*Protereunetes brevipes*	.	.	.	.	.	.	x	.	.	x	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.
97	*Tyroborus lini*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
98	*Brachychthonius scalaris*	.	.	.	.	**3**	**31**	.	*5*	.	.	**6**	.	**12**	**7**	.	.	.	.	.	.	.	.	.	.	.	**3**	**7**	.	.
99	*Tectocepheus velatus*	.	.	.	.	.	*1*	x	*1*	.	.	.	*2*	x	**1**	.	.	.	.	x	x	.	.	.	.	.	.	.	*1*	.	
100	*Hermannia reticulata*	.	.	.	.	.	.	.	*6*	.	.	x	.	x	x	.	**4**	.	.	.	x	.	.	.	.	.	.	.	.	.
101	*Ceratoppia sphaerica*	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
102	**Folsomia sensibilis*	.	.	.	.	1	.	.	*1*	.	*2*	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
103	**Willemia anophthalma*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
104	**Micranurida pygmaea*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
105	**Isotoma viridis*	*1*	.	.	.	*2*	**3**	.	*1*	x	*1*	*1*	*x*	*1*	1	1	.	.	.	1	.	.	.	1	.	.	.	.	x	
106	**Onychiurus macfadyeni*	*3*	.	.	.	.	.	.	.	1	x	**3**	**3**	*1*	**18**	**17**	**16**	x	.	x	.	.	.	.	.	.	.	*1*	.	
		S	C	C	C	B	B	B	B	Q	B	B	B	B	B	B	B	D	H	N	A	E	E	E	E	J	F	H
		9	1	2	3	8	5	13	7	7	9	3	10	4	2	1	11	12	1	1	3	3	2	4	6	4	4	2

pes (*numbered in Roman figures*)

266 and 281)



Folsomia sensibilis Kseneman [102]. Found in types II, IV and V, nearly all sites having a closed vegetation with moss and higher plants. However, accidental individuals occur in closed moss only (K4) and in the peculiar locality J3 (see p. 279). Fine soil particles dominate in all localities which are sheltered and with not less than 7% plant matter.

Isotoma notabilis Schäff [78]. Constant only in fauna types VI and V, but present also in B1 and B4 of fauna II, which, like type VI, have grasses. This distribution is the nearest approach among the Collembola to that of the oribatids of fauna V but the factors determining its distribution are not clear.

Isotoma viridis Bourlet [105]. This species is nearly ubiquitous and lives on, rather than in the soil. It mainly favours fauna types II, V and VI and areas of moderate moisture.

Isotomiella minor (Schäff.) [80]. Confined to areas of closed vegetation including moss, this species is constant only in type V faunas with single casual individuals in IV and VI.

Archisotoma besselsi Pack. [6]. This species is present or constant in the sea-shore localities where it was also found by Hammer (1938) and is regarded as the differential species for the type I*b* fauna. Casual individuals also occurred in A4, N4 and S2.

Neelus minimus Willem. [79]. Only 'present' in fauna V, but casuals occur also in faunas II, IV and VI. The vegetation is nearly always closed and the sites sheltered. Not less than 7% plant matter in the soil.

Sminthurinus concolor Meinert. [23]. Casual individuals in L1 (type IV) and S3 (type V) as well as the distribution in the type II fauna show fouling to be irrelevant as a factor for this species. It does not occur where the soil has coarse particles, where there is less than 7% plant matter nor in the absence of a closed vegetation; it also appears to avoid places where Enchytraeidae occur. Apparently rather less widespread than in East Greenland (Hammer 1938).

VARIATION IN TIME OF THE FAUNA OF ONE LOCALITY

Samples were taken at weekly intervals at one sampling station (B2) in order to obtain a general idea of whether it would be permissible to compare the samples from all Jan Mayen localities with one another despite the fact that the sampling period occupied some 5 weeks. The results of this experiment are shown in Table 3, the same conventions being used as for Table 1. It will be evident that, on the whole, the same fauna is represented in all the samples and that none of the constant species completely disappear from one week to the next. However, many of the casual species are present on only one or two occasions, and there does appear to be a distinct trend for the adults of *Xenylla humicola*, *Brachychthonius scalaris*, *Oppia neerlandica* and *Folsomia bisetosa* to become less abundant as the season progresses, and particularly on the last date. This supports the contention, elaborated on p. 266, that exact abundance figures have little significance when comparisons are made between different localities although the comparison of faunas as a whole on the basis of sets of five samples would appear to be justified, at least over the first monthly period.

Table 3. *Weekly samples at station B2*

(For conventions used see Table 1.)

	July		August	
	21	30	7	15
Ameronothrus lineatus	×	.	.	.
Brachychthonius scalaris	5	4	12	*2*
Oppia neerlandica	15	7	5	×
Tectocepheus velatus	.	×	*3*	×
Hermannia reticulata	.	×	×	.
Zercon franzi	2	5	3	*2*
Cyrtolaelaps mucronatus	×	1	.	.
Microtydeus similis	×	.	×	.
Rhagidia gelida	5	×	*1*	×
Epodes variegatus	1	.	.	.
Cocceupodes curviclava	*2*	.	*4*	*1*
Protereuntes börneri	.	.	1	×
Nanorchestes arboriger	*3*	×	8	2
Penthaleus bipustulatus	*1*	×	*2*	×
Bryobia graminum	*4*	1	.	.
Oudemansium domesticum	.	1	.	.
Xenylla humicola	160	29	23	8
Onychiurus macfadyeni	12	30	25	6
Isotoma viridis	.	*1*	1	1
Folsomia sexoculata	.	×	.	.
F. bisetosa	20	2	11	×
Tullbergia krausbaueri	*6*	2	3	4
T. arctica	*4*	1	3	3
Pygmephorus cultratus var. *minor*	.	×	.	×

COLLECTIONS OTHER THAN THOSE OF THE SOIL FAUNA

A number of collections for invertebrate animals were made by means of a sweep net and an aspirator on the general ground surface, under stones and in association with the abandoned living huts. These revealed no new species for the island with the single exception of a parasitic hymenopteran, *Plectiscus* sp. which was found in a shed which had been used as a pony stable, with specimens of the two *Trichocera* species and *Scatophaga varipes*. The same four species of spider as were previously found by Bristowe (1925) were recorded and their distribution is discussed by Bristowe (1948). The distribution of the Diptera and Hymenoptera is shown in Table 4. Dr Strenzke, who kindly identified the Diptera larvae extracted from the soil samples, found the species shown in Table 4; he is of the opinion that the *Camptocladius* of earlier authors are the *Smittia* of his lists and also that found as an adult on the hilltop above The Pillar.

The only places where Diptera were found in considerable numbers were in the camp region (mainly *Trichocera* species and *Scatophaga*), in the caves formed under the hard laval crust of the volcanic desert to the north-east of the South Lagoon (mainly *Cricotopus basalis*), and visiting *Cerastium alpinum* (mainly *Limnophora megastoma*). The caves appear at first sight to be a rather barren place, but from the fairly rich flora and presence of bird feathers in them it seems possible that sea birds may shelter there in stormy weather. None of the flies associated with the camp site

are restricted to that area, the Nematocera having their natural habitat in the caves while *Cynomya* and *Scatophaga* are very widely distributed.

Table 4. *Distribution of Diptera and Hymenoptera in Jan Mayen*

	Muscidae		Other Cyclorrhapha				Nematocera					Hymenoptera	
	Acropterna	*Limnophora megastoma*	*Cynomya mortuorum*	*Scatophaga nigripes*	*Scatophaga varipes*	*Exechia frigida*	*Smittia* sp.	*Sciara* sp.	*Cricotopus basalis*	*Trichocera lutea*	*Trichocera maculipennis*	*Stenomacrus* sp.	*Plectiscus* sp.
ssingdalen, fjaeldmark:													
(*a*)	.	.	.	.	.	×	.	.	.	.	.	.	.
(*b*)	.	.	.	.	×	×	.	.	×	.	.	.	.
(*c*)	.	.	×	×	.	.	.	.	.	.	.	.	.
he Pillar, sheltered south-facing vegetation	.	.	×	×	×	.	.	×	.	.	.	×	.
bandoned camp:													
Barracks	.	.	.	.	×	.	.	.	.	×	×	.	.
Radio hut	.	.	×	.	×	.	.	.	.	×	.	.	.
Barracks	.	.	.	.	×	.	.	.	.	×	×	.	.
Pony stable	.	.	.	.	×	.	.	.	.	×	×	×	×
Rubbish heap	.	.	×	.	×	.	.	.	.	.	.	.	.
Latrines	.	.	.	.	×	.	.	.	.	.	.	.	.
Vildberg, summit	.	.	.	.	.	.	.	.	.	.	.	×	.
olcanic desert caves:													
(*a*)	.	.	.	.	.	.	.	.	×	×	×	.	.
(*b*)	.	.	.	.	×	.	.	.	×	.	.	.	.
(*c*)	.	.	.	×	×	.	.	×	×	.	.	.	.
each S.E. of North Lagoon													
(*a*)	.	×	.	.	.	.	.	.	×	.	.	.	.
(*b*)	.	.	×	.	×	.	.	.	.	.	.	.	.
erastium on Mohnberg:													
(*a*)	.	×	.	.	.	.	.	.	×	.	.	.	.
(*b*)	.	.	.	×	.	×	.	.	.	.	.	.	.
ea beach, Seven Hollanders Bay	.	.	.	×	.	.	.	.	.	.	.	.	.
ogelberg summit (cf. Q series)	.	.	.	×	.	×	.	.	.	.	.	.	.
ishburn Valley, *Taraxicum*	×	.	×	.	.	.	.	.	.	.	.	.	.
illtop above The Pillar, on stones	.	.	.	.	.	.	×	.	.	.	.	.	.

CONCLUSIONS

(*a*) *Sampling and analytical technique*

It may well be contended that the same, or equally valid information could have been obtained by any good naturalist without such elaborate methods. On the one hand it would be quite obvious to such a naturalist that *Archisotoma besselsi*, for instance, is a differential species for the non-fouled sea-shore sites and that *Pygmephorus spinosus* is one for grass plots in Jøssingdalen. On the other hand, it is also true that so much information, from so many localities and concerning so many species, is very difficult to assimilate, and that some at least of the fauna types would probably be overlooked,

and that the affinities between them would probably be missed or obscured by subjective impressions. Types III and VII may not be very clearly separated in the present analysis, but at least it is possible to compare the available evidence and to indicate types of habitat in which further study would help to resolve their status. It is difficult without some sort of analysis to draw boundaries between fauna types, and the method used here seems to do this with a minimum of calculation and to have indicated boundaries which were not apparent at first sight. The rather close correspondence demonstrated in section IV with Russell & Wellington's floristic classification provides some evidence for an objective basis for such a classification.

Gisin (1947, pp. 63–7) considers in some detail the question of correspondence between faunistic and floristic groupings and quotes the opinions of authors who take up all possible positions on this question. On the basis of his own data Gisin arrives at the same conclusions as in this paper, namely that there is a considerable measure of correspondence, provided that both analyses have been adequate. He notes a tendency for the more extreme plant associations to correspond most strictly to animal associations, and he attributes many cases of imperfect correspondence in successional vegetation systems to the greater mobility of the fauna, allowing it to respond more rapidly than the flora.

Lessons which are indicated by this study include the desirability of a pilot survey (demanding more time and microscope facilities) in order to decide the size of sample to be used in different localities. A more rewarding analysis of all fauna IV samples would have resulted from the use of 100 cm.^{2} samples, but to have used this size for the fauna II and fauna V samples would have involved unnecessarily bulky apparatus and a waste of labour. It is possible that in a further sampling on Jan Mayen the information already gained would make a pilot survey unnecessary.

The value of precise counts may be questioned at this stage. The extraction methods in use are known to be inaccurate, and populations can be assumed to vary greatly both in space and in time (see p. 291 and Macfadyen 1953). There is therefore much to be said for using some index of abundance such as is used by Gisin (1952) provided counting labour is thereby appreciably reduced. Except in the unlikely event of the abundance numbers being required for a productivity study the only possible objection to such methods is that mean densities for a number of samples cannot be calculated. Errors due to the inequitable extraction of different species are likely to outweigh by far inaccuracies of estimation. On the other hand, should the intensive activity now being devoted to quantitative extraction methods result in the invention of a universal field method the interest of exact figures from a productivity point of view should not be forgotten.

In conclusion it is submitted that a faunistic analysis based on vicariant or differential species can, with the qualifications already made, permit the use of material obtained under expedition conditions for ecological generalizations which are likely to be more informative than those based solely on observation. It will only be possible to assess their wider significance when a number of such surveys for different localities and on separate occasions can be compared with one another.

(*b*) *The fauna of Jan Mayen*

As a census of the arthropod fauna of a small arctic island this study has contributed little to our knowledge of the larger insects and spiders. However, it has more than doubled the list of Collembola and multiplied eightfold that of Acari, thereby permitting comparisons to be made with Iceland and Greenland. All but three of the Nematoda listed by Dr Allgén are new to Jan Mayen. From an ecological point of view, although certain habitat types evidently require more thorough study, a foundation has been laid for a system of soil-inhabiting communities. While this information could be made much more precise, the value of doing so by methods which ignore the biology of the animals and the role they play in their communities seems doubtful. In fact the relative poverty of this and other arctic faunas and the simplifications imposed by rigorous physical conditions make arctic soils particularly attractive for combined studies of plant succession and soil micro-organisms. Russell & Wellington (1940, p. 287) remark that the main factor limiting plant growth on the island appears to be low bacterial activity. Wilson disputes this (1948 and personal communication) and considers sunlight, low temperature and exposure to be important factors. Whatever the cause it was indeed striking to observe in 1947 that wheel tracks made in the moss two years previously looked almost as clear as if they had just been made, new growth of the mosses having quite failed to obscure them. Remembering the tendency for botanists, despite the teachings of Waksman, to attribute all soil breakdown activity to 'bacteria', and allowing the surprisingly rich fauna some part in these processes, a study of the role of these forms in arctic soils would appear to be a most promising undertaking. The tentative comparisons made (see L series of samples) with Wilson's study of 'fairy rings' in mosses and the line of thought suggested by the peculiar samples discussed on pp. 279–80 indicate that studies on means of distribution of the microfauna, the rate of exploitation of micro-habitats and on contributions to the breakdown processes of decaying vegetation would be profitable ways in which to start such an investigation.

ACKNOWLEDGEMENTS

This work would not have been possible without the generous and time-consuming help of taxonomic experts; Dr Allgén counted and identified all the Nematoda, Dr Bristowe the spiders, Dr Hobby the adult Diptera, Dr Strenzke the Diptera larvae and Dr Stroyan the Aphidae. These gentlemen examined the whole of their respective materials and are solely responsible for the identifications. In the case of the Collembola and the Acari the material, amounting to about 10,000 specimens in each case, did not permit this course and, after sorting a subsample I sent representative material to Dr Gisin and to my good friend and mentor Dr Turk; their determinations were followed by further sorting and further checking of doubtful specimens. Since these two experts examined but a fraction of the material I must take responsibility for part of the determinations although they both saw specimens of all the species reported. The independent papers by the above authorities are listed in the bibliography (Allgén 1953, Bristowe 1948, Doncaster & Stroyan 1952, Gisin 1953). I wish here to express my grateful thanks to these kind gentlemen who have, between them,

determined the following 163 species new to the island and eighteen species new to science:

	New to Jan Mayen	New to science
Nematoda	41	2
Collembola	13	2
Acari	104	13
Aphidae	3	1
Hymenoptera	1	—
Diptera	1	—
Total	163	18

My gratitude is also due to many correspondents and colleagues who have made comparisons with other holarctic faunas possible, especially Drs Forsslund, Strenzke, Hammer and Turk, and to Mr Elton, Drs Gisin, Strenzke and Wilson who took much trouble over reading and correcting the typescript. To the earlier members of Oxford University Exploration Club and its benefactors, and to Dr A. J. Marshall, the outstanding leader of the 1947 Expedition to Jan Mayen, I owe an incalculable debt which includes far more than is implied by the mere organization which allowed me to visit this extraordinary island. Mr Charles Elton, F.R.S., has provided generous facilities and time for work on the material and has, as always, given invaluable advice and criticism at all stages of the work.

REFERENCES

Agrell, I. (1941). Zur Ökologie der Collembolen: Untersuchungen im Schwedischen Lappland. *Opusc. ent.* (Suppl.) **3**, 1–236.

Agrell, I. (1945). An objective method for the characterization of animal and plant communities. *K. fysiogr. Sällsk. Lund. Förh* **15**, 1–15.

Agrell, I. (1948). A dubious biocenological method. *Opusc. ent.* **13**, 57–8.

Allgén, C. (1953). Terrestrial nematodes from Jan Mayen. *Ann. Mag. Nat. Hist.* (12) **6**, 665–89.

Braun-Blanquet, J. (1932). *Plant Sociology*. New York.

Becher, (1886). *Österreichische Polarstation Jan Mayen: Insekter*. Vienna.

Bristowe, W. S. (1922). The insects and arachnids of Jan Mayen. *Proc. Camb. Phil. Soc.* **21**, 38–43.

Bristowe, W. S. (1925). The fauna of the arctic island of Jan Mayen and its probable origin. *Ann. Mag. Nat. Hist.* (9), **40**, 480–5.

Bristowe, W. S. (1948). Spiders from the arctic island of Jan Mayen. *Proc. Zool. Soc. Lond.* **118**, 223–5.

Doncaster, J. P. & Stroyan, H. L. G. (1952). A new subgenus and new species of aphid from Jan Mayen Island. *Ann. Mag. Nat. Hist.* (12), **5**, 984–7.

Edwards, F. W. (1923). On the nematocerous Diptera of Jan Mayen Island. *Ann. Mag. Nat. Hist.* **11**, 235.

Elbo, J. G. (1953). The war in Jan Mayen 1940–45. *Polar Rec.* **6**, 735–9.

Elton, C. S. (1927). *Animal Ecology*. London.

Gisin, G. (1952). Oekologische Studien über die Collembolen des Blattkomposts. *Rev. suisse Zool.* **59**, 543–78.

Gisin, H. (1943). Ökologie und Lebensgemeinschaften der Collembolen in schweizerischen Excursionsgebiet Basels. *Rev. suisse Zool.* **50**, 131–224.

Gisin, H. (1947). Analyses et Synthèses biocénotiques. *Arch. Sci. phys. nat.* **29**, 42–75.

Gisin, H. (1949). L'écologie. *Acta biotheor., Leiden*, **9**, 89–100.

Gisin, H. (1951). La biocénotique. *Ann. Biol.* **27**, 81–88.

Gisin, H. (1953). Collembola from Jan Mayen island. *Ann. Mag. Nat. Hist.* (12), **6**, 228–34.

Haarløv, N. (1947). A new modification of the Tullgren apparatus. *J. Anim. Ecol.* **16**, 115–21.

Hammer, M. (1937). A quantitative and qualitative investigation of the microfauna communities of the soil at Angmagssalik and in Mikisfjord. *Medd. Grønland*, **108** (2), 53 pp.

Hammer, M. (1938). Zoology of East Greenland: Collemboles. *Medd. Grønland*, **121** (2), 1–42.

Hammer, M. (1944). Studies of the Oribatids and Collemboles of East Greenland. *Medd. Grønland,* **141** (3), 1–210.

Hammer, M. (1946). The Zoology of East Greenland: Oribatids. *Medd. Grønland,* **122** (1), 39 pp.

Hammer, M. (1952). Investigations on the Microfauna of Northern Canada: Part 1 Oribatidae. *Acta arct., Kbh.,* **4**, 1–108.

King, A. (1939). The Imperial College expedition to Jan Mayen. *Geogr. J.* **94**, 115–30.

Kontkanen, P. (1950*a*). Quantitative and seasonal studies on the leafhopper fauna of the field stratum on open areas in North Karelia. *Ann. Soc. (bot.-zool.) Soc. zool.-bot. fenn., Vanamo,* **13**, 1–91.

Kontkanen, P. (1950*b*). Sur les diverses méthodes de groupement des recoltes dans la biocénotique animale. *Vie et Milieu,* **1**, 121–30.

Kulczynski, St M. (1927). Die Pflanzenassoziationen der Pienen. *Bull. int. Acad. Cracovie (Acad. pol. Sci.),* **2**, 27–204.

Linnaniemi, W. M. A. (1935). Collembolen aus Spitsbergen, Insel Hopen, Kong Karis' Land und Jan Mayen eingesammelt von norwegischen arktischen Expeditionen. *Norsk ent. Tidskr. Oslo,* **3**, 379–81.

Macfadyen, A. (1953). Notes on methods for the extraction of small soil arthropods. *J. Anim. Ecol.* **22**, 65–77.

Marshall, A. J. (1948). The Oxford University Expedition to Jan Mayen, 1947. *Bull. Ox. Univ. Explor. Cl.* **1**, 7–10.

Overgaard-Nielsen, C. (1949). Studies on the soil microfauna: 2. The soil inhabiting nematodes. *Nat. Jutland,* **2**, 1–131.

Polunin, N. (1951). The real arctic: suggestions for its delimitation, subdivision and characterization. *J. Ecol.* **39**, 308–15.

Renkonnen, O. (1938). Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. *Ann. (bot.-zool.) Soc. zool.-bot. fenn., Vanamo,* **6** (1), 277 pp.

Russell, R. S. (1940*a*). Physiological and Ecological Studies on an Arctic vegetation. 2. The development of vegetation in relation to nitrogen supply and soil micro-organisms on Jan Mayen Island. *J. Ecol.* **28**, 269–88.

Russell, R. S. (1940*b*). Physiological and Ecological Studies on an Arctic vegetation. 3. Observations on carbon assimilation, carbohydrate storage and stomatal movement in relation to the growth of plants on Jan Mayen Island. *J. Ecol.* **28**, 289–309.

Russell, R. S. & Wellington, P. S. (1940). Physiological and ecological studies on an arctic vegetation. 1. The vegetation of Jan Mayen Island. *J. Ecol.* **28**, 153–79.

Salt, G. (1952). The arthropod population of the soil in some East African pastures. *Bull. Ent. Res.* **43**, 203–20.

Sellnick, M. (1940). Die Milbenfauna Islands. *Göteborgs VetenskSamh. Handl.* (B) **6**, (14) 1–130.

Sørensen, T. (1948). A method of stabilizing groups of equivalent amplitude in plant sociology based on the similarity of species content and its application to analyses of the vegetation on Danish commons. *Biol. Skr.* **5** (4), 1–34.

Strenzke, K. (in press). Oribatiden aus West Grönland.

Summerhayes, V. S. & Elton, C. S. (1928). Further contributions to the ecology of Spitsbergen. *J. Ecol.* **16**, 193–268.

Tansley, A. G. (1923). *Practical Plant Ecology.* London.

Thor, S. (1930). *Skeifter om Svalbard of Ishavet,* no. 27.

Tuomikoski, R. (1942). Zur Methodik der Pflanzensoziologischen Systematik. *Ann. (bot.-zool.) Soc. zool.-bot. fenn., Vanamo,* **17**, 1–200.

Tuxen, S. L. (1944). The hot springs of Iceland. *The Zoology of Iceland,* **1** (11), 1–206.

Wahlgren, E. (1900). Collembola während der schwedischen Grönlands-Expedition 1899 und auf Jan Mayen und Ost-Grönland eingesammelt. *Öfvers. VetenskAkad. Förh., Stockh.,* no. 3, 353–76.

Watt, A. S. (1947). Pattern and process in the plant community. *J. Ecol.* **35**, 1–22.

Wilson, J. W. (1948). Limits of endurance: plant life at Jan Mayen. *Sci. News.* **9**, 75–83.

Wilson, J. W. (1951). Observations on concentric 'Fairy rings' in arctic moss mat. *J. Ecol.* **39**, 407–16.

Wilson, J. W. (1952). Vegetation patterns associated with soil movement on Jan Mayen Island. *J. Ecol.* **40**, 249–64.

Wordie, J. M. (1922). Jan Mayen Island. *Geogr. J.* **77**, 180–195.

THE BIOLOGY OF THE MARINE PLANKTONIC COPEPODS OF SCORESBY SOUND, EAST GREENLAND

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(With 16 Figures in the Text)

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INTRODUCTION

In a previous paper (Digby 1953) an account was given of the cycle of marine plankton production and of the phytoplankton succession throughout the year at a station in polar surface water. The account was based on a series of quantitative samples taken from August 1950 to August 1951, at intervals of a fortnight in winter and a week in summer, in Rosenvinge Bay, Scoresby Sound, East Greenland. This paper describes the life-histories of the copepods from the same material. About half the plankton, by bulk, consisted of copepods, the remainder being more gelatinous organisms of one sort or another. As the organic content of these other organisms is slight, the copepods were, from the point of view of the turn-over, by far the most important group of zooplankton animals.

In temperate waters the various species of plankton copepods pass through several generations a year (Nicholls 1933; Marshall, Nicholls & Orr 1934; Fish 1936*a*, *b*, *c*; Wiborg 1944; Marshall 1949; Digby 1950; Deevy 1952*a*, *b*). The different generations are usually incompletely separated, breeding becoming more or less continuous during the summer and the later part of the year. Before 1938 work on the copepods of the high arctic had been restricted almost entirely to systematic investigations, the collections, with the exception of those of Vanhöffen (1897) from Little Karajak Fiord on the west coast of Greenland having been taken only in summer. Reference may be made to the papers of Jespersen (1939*a*, *b*) for details of the occurrence of the various species in East Greenland. In 1938 Ussing published the results of his work on the collections of plankton made in East Greenland throughout the year during Koch's Three-Year Expedition of 1931–34. He showed that most of the common copepods had one generation a year and gave details of the seasonal occurrence of the various stages.

Now it is a little difficult to explain how the copepods live through the winter in the arctic at all, for if they are exclusively filter-feeding forms, as so much experimental work seems to show, and if our estimates of their metabolic rate are correct, they would not be able to survive the winter without reducing this rate. Whether they do so or not we do not know, but even if they did this would not allow any growth. Nevertheless, Ussing has reported growth over a stage or two in *Calanus*, the production of nauplii in *Microcalanus* in winter, and the reproduction of *Oithona* at all seasons, the most productive spawning being that of September and October. In my last paper (Digby 1953) I showed that from the rate of decrease of the biomass over winter the food requirements of the copepods at the summer metabolic rate would be adequately satisfied through the year if some process existed whereby a population of apparent filter-feeders could live on its own members, allowing the surviving individuals to grow and possibly reproduce in the absence of phytoplankton. We therefore need to know in a little more detail to what extent growth of the individual can go on in the virtual absence of phytoplankton, and to what extent nauplii and young stages which might be expected to be the first to suffer from predation, are present through winter.

In the present material from Scoresby Sound, it was shown that the curve of the biomass of the copepods did not decline steadily throughout winter, but decreased sharply in early autumn, remained fairly level in late autumn and winter, and fell off steeply again in early spring, thus giving the appearance of an increase centred over mid-winter superimposed on a generally declining stock. The biomass is a function of both abundance and size. Ussing has shown that the copepods could be separated into two groups, one present at the surface in summer and sinking to the depths in winter represented by *Calanus* and *Pseudocalanus*, the other present in the surface in winter and sinking to the depths in summer represented by *Metridia*, *Microcalanus* and *Pareuchaeta*. The suggested mid-winter increase in biomass proved to be due not only to the appearance in the nets of the winter forms, the *Metridia* group, but also to an increase in size of the later stages of *Calanus* over mid-winter.

In temperate waters, although the copepods change in size through the year it is difficult to say to what the size-change may be attributed because of the complication of factors. In arctic waters the copepods are under almost experimental conditions, in that the duration of phytoplankton production is short and is followed by a long period of almost complete absence of plant material in the water. The temperature of the sea is almost constant throughout the year, compared with the range of variation common in more southern waters. Ussing described how the various stages increased in size over the period of phytoplankton production, and as the temperature varied but little, this size increase must have been due almost entirely to the phytoplankton. He concluded that this relationship gave rise to the much discussed bimodal size-distribution of late stages of *Calanus* and the unimodal size-distribution of *Pseudocalanus* and *Metridia* by the individuals produced under different conditions of nutrition co-existing in the one case but not in the other. From his series of measurements he concluded that the size attained after a moult was affected by two factors, the size of the preceding stage and the state of nutrition at the time of moulting. It seemed a little difficult to account for the apparent mid-winter size-increase of *Calanus* on these grounds alone.

In order to gain some more information on these points the life-histories of the copepods were investigated from the Scoresby Sound material. Species which occurred in numbers sufficient for conclusions to be drawn regarding their life-histories were as follows:

Calanus finmarchicus (Gunnerus)
C. hyperboreus Krøyer
Pseudocalanus minutus (Krøyer)
Oithona similis Claus
Oncaea borealis G. O. Sars
Microcalanus pygmaeus G. O. Sars
Metridia longa (Lubbock)
Pareuchaeta sp., probably *norvegica* (Boeck) or *glacialis* (H. J. Hansen)

A few species were taken in small numbers. They comprised:

Bradyetes brevis Farran
Acartia longremis (Lilljeborg)
Heterorhabdus norvegicus (Boeck)
Oithona atlantica Farran
Oithona sp. ? *nana* (Giesbrecht)
Oncaea sp. ? *minuta* Giesbrecht

In addition to the above, the harpacticids *Microsetella norvegica* (Boeck) and *Ectinosoma* sp. were taken in the samples up to a maximum of about 20 m.^{3}, but these were not assessed quantitatively.

MATERIAL AND METHODS

In the previous paper a description was given of the way in which two nets, of fine and coarse mesh, 200 and 48½ meshes per in. and 12·5 and 50 cm. diameter at the mouth respectively, were fitted with meters and were fished vertically through the upper 50 m. of water, the catches of the two nets being combined to give quantitative values for the larger and smaller organisms together.

After separating by rinsing through sieves and subsequently weighing, the fine material and the medium and coarse copepod fractions were subsampled separately for counts by an adaptation of the dilution method described by Russell (1931).

In the case of the fine net samples, the fine fraction was subsampled to give quantities corresponding as a rule to 50, 150, 300, 500, 1000 ml., etc. These fractions were so chosen that the quantities of water represented by any number which were examined, starting from the smallest and working upwards, would always add up to a convenient fraction or multiple of 1 m.^{3}. Smaller quantities were taken for diatom and nauplii counts, then progressively larger quantities for less abundant nauplii and for the copepodites. The medium fraction was subsampled in much the same way, which commonly involved examining between a half and one-twentieth of the fraction in detail and searching through further subsamples for additional specimens for abundance figures or for size-measurements. The subsamples were such that in each of the fractions, the fine and medium material, between 200 and 500 individuals were examined. The coarse fraction was examined *in toto*, the numbers being small.

The coarse net samples were treated in much the same way, quantitative subsamples containing 200 to 500 individuals being examined from each of the two fractions, medium and coarse, obtained from them. The fine and medium fractions were spread on a slide ruled in 0·1 in. squares and were examined under a microscope with a mechanical stage, measurements being made by an eye-piece micrometer in which each division represented 20μ. The coarse material was examined in a Bogorov tray (Russell 1931) under a low-power binocular, measurements being made by micrometer eye-piece in which a division represented 70μ. The division of the samples into

fractions by rinsing through sieves, as described in the previous paper, proved very convenient, the medium fraction copepods (those which could be rinsed through a sieve of 27 meshes/in.) being of convenient size to measure with the microscope but too small for the binocular, and the coarse fraction copepods (those retained by a sieve of 27 meshes/in.) being too large for the microscope but of convenient size for the binocular. All copepod measurements refer to the length of the cephalothorax.

A net is only quantitatively accurate over a certain size-range of organisms. Smaller organisms pass through the meshes, organisms which cannot pass through the meshes and are too small to escape by rapid movement are caught quantitatively, and those which are large enough to escape the net are only caught occasionally. The figures for *Pseudocalanus* indicated that more were caught per cubic metre by the medium than by the fine net, which probably means that copepods even as small as late stage *Pseudocalanus* may be lost by escape from the path of the fine net with its 12·5 cm. aperture. In the case of the larger copepods a proportion of the larger *Calanus* were probably lost from the path of the 50 cm. diameter net. The quantitative values given are subject to these limitations.

ABUNDANCE, SIZE AND LIFE-HISTORIES

(*a*) Calanus finmarchicus (*Table 1*)

As noted by Ussing the smaller *C. finmarchicus* is distinguishable from the larger *C. hyperboreus* by size down to and including copepodite stage II, but in stage I, as shown in the size-group diagram in Fig. 2, the two species merge in size and cannot be distinguished.

In the calanid nauplii (see the figures given by Oberg 1906, and Lebour 1916) three obvious size-groups were evident. The smallest, common early in the year, could be followed on in the life-history diagrams to the copepodites of *Microcalanus*, the middle one to those of *Pseudocalanus*, and the large one to the two species of *Calanus*, *C. finmarchicus* and *C. hyperboreus*. This group of large nauplii could again be divided on several occasions into a larger and a smaller form, as described by Sømme (1934). Sømme showed the two sizes of the various stages of *Calanus* material in Norwegian waters to belong to the two different species, but in view of the way in which the size-groups of the two species in this Greenland material were separable as stage II copepodites but were indistinguishable as stage I, it appears more likely that here the differences of size of the nauplii did not necessarily correspond to the distinction between the two species but were caused by some other factor, such as, perhaps, the amount of food available in different blocks of water at the time of hatching. The nauplii and copepodite stage I of the *Calanus* material are therefore grouped together in the abundance figures and diagrams.

In Fig. 1 is shown the abundance of *C. finmarchicus* and *C. hyperboreus*. The graphs for nauplii and copepodites stage I include both of these species together while the later stages are separated. Nauplii of the two species were present from April until October, with a maximum from June to August. Copepodites of stage I (*C. finmarchicus* and *hyperboreus* together) appeared at the beginning of June, were common until October with a maximum in July and August, and were absent from December until April. Copepodites of stages II–V, and adult females of *C. finmarchicus*, were

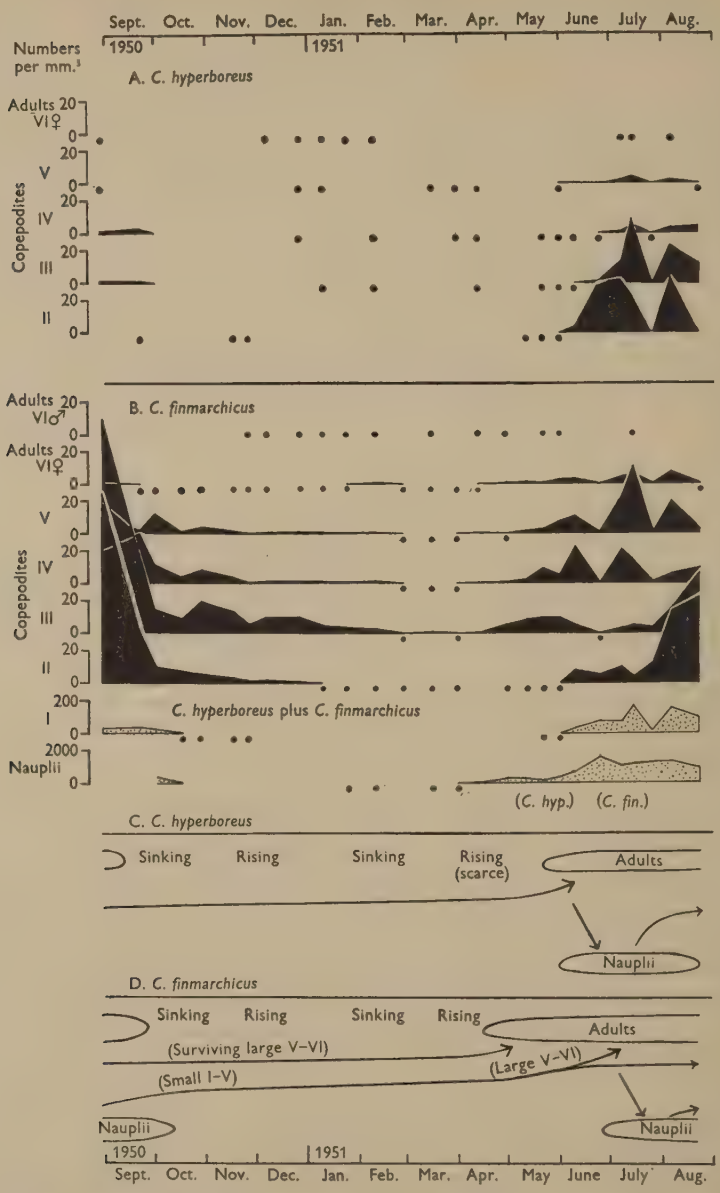

Fig. 1. *Calanus finmarchicus* and *C. hyperboreus*. A, *C. hyperboreus*, abundance of stages II–VI. B, *C. finmarchicus*, abundance of stages II–VI; and *C. finmarchicus* and *C. hyperboreus* together, abundance of nauplii and stage I. Scale of stage I is one-tenth, of nauplii one-hundredth, that of remaining stages. Dots indicate specimens present but in numbers less than 50, 5 and 0·5/m.³ for nauplii, stage I and stages II–VI respectively. C, interpretation for *C. hyperboreus*. D, Interpretation for *C. finmarchicus*.

present all the year round, although scarce in winter. Stage II appeared at the same time but had a rather longer period of abundance than stage I, that is until December, with a peak in August and September. Stage III appeared before stages I and II, having a period of abundance in May separated by a short gap in June from another period of abundance extending from August until January. Stages IV and V were

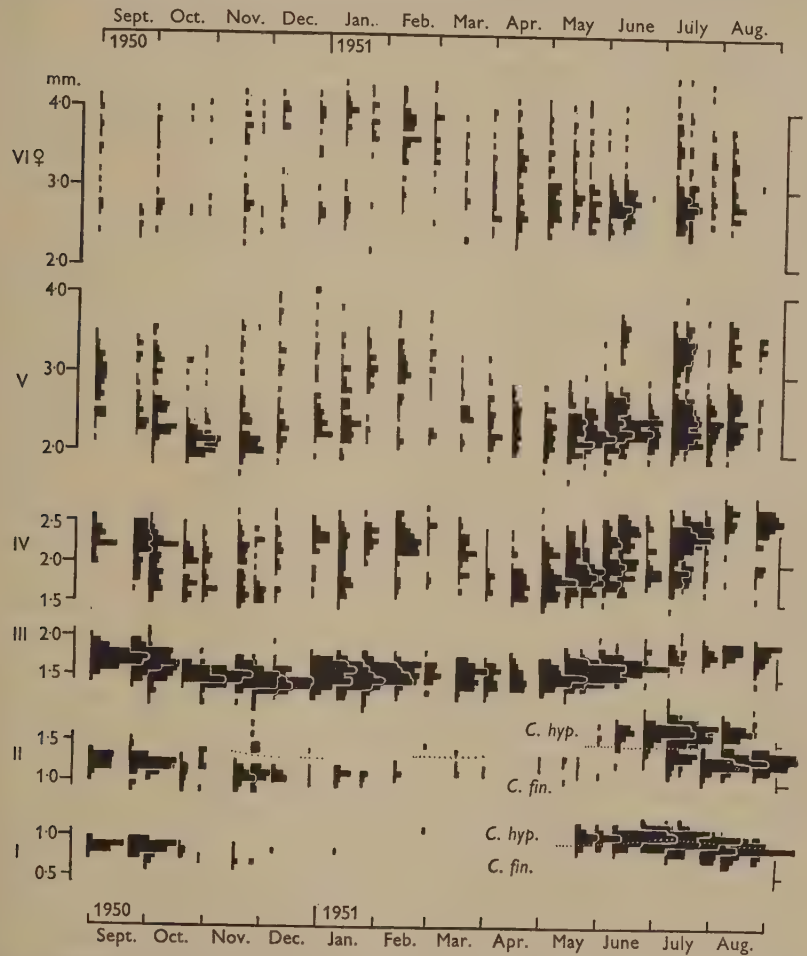

Fig. 2. *Calanus finmarchicus*, size-groups of stages I–VI. Groups for stages I and II include the larger *C. hyperboreus*, the probable line of demarcation between the two species being shown by a dotted line.

present in abundance from May to November and the adult females from May to September. Adult males were taken sparsely in winter, spring and early summer, from November through to July, none appearing in the nets in August, September and October.

In the size histograms (Fig. 2) the graphs for stages I and II include those stages of both *C. finmarchicus and C. hyperboreus*. In stage I the overlap of the size of the two

species was such that the two were inseparable, but in stage II the graphs are obviously bimodal, and the two groups can be followed through to the late copepodite stages where the individuals are distinct on morphological grounds. The possible line of demarcation between the two species is shown by a dotted line in each case. The line of demarcation obviously varies with the season. There were two size maxima. One occurred during the phytoplankton increase from May to August, and was obvious in all stages, the summer specimens of stages IV–V appearing as separate groups of larger size than the winter specimens. An increase in size of the females in the surface waters at that time was scarcely evident in the size-histograms, but a slight rise can be seen in the mean size-graph (Fig. 16) for July and August. Adult males were present in insufficient numbers for any seasonal change in their size to be evident. A lag of perhaps a month is evident in the mean size-graphs between the time of attainment of maximum size of stages III and V. The other size-increase was during the winter months, centred over the end of January. It affected stages IV–VI and there was a suspicion of it in stage III. It was caused by the appearance of large specimens of these stages, and there was no lag between the time of attainment of maximum size in successive stages such as was seen in the summer size-increase.

On first inspection of the abundance graph, the life-history appears simple. Stages III–VI, which had been present in the depths all winter, began to rise from below the 50 m. level in April. This increase in late stages at this time must have been due to rising of the stock because it was not accompanied by, or preceded by, a commensurate increase in nauplii and stages I and II. Stage VI was already mature, and stages III–V advanced towards maturity; a line of development, rather ill-defined, can be seen from the first stage III in April and May to stage VI in June–July–August. These adults were responsible for the production of the single summer brood of nauplii. The nauplii shown in Fig. 1, present from April onwards, belonged to the two species of *Calanus*, the early ones probably nearly all *C. hyperboreus* and the later probably nearly all *C. finmarchicus* because when they had developed to stage II where the two species are separable on size there was a difference of 6 weeks between the peaks of each. These nauplii of *C. finmarchicus* developed to stage I in June–July–August and to stage III in July to September. The line of development beyond stage III was obscured by the overall decline in the stock through mortality and through sinking to lower levels, so it is not possible to say how fast the development proceeded. The more advanced members of the stock no doubt developed to stages IV and V, and perhaps some of them to adult males and females in the autumn, and it is certain that individuals of stages I and II developed as far as stage III during the winter, because stage I disappeared and stage II became scarce in the autumn, and neither of them appeared again until the new generation began to develop in the following summer. Stage III remained comparatively abundant in winter, either because development of stages I and II proceeded no further than that of stage III or else because it did not sink to the depths to the same extent as did the later stages—perhaps for both reasons. It would therefore seem probable that most of the stock developed over one, or possibly two, stages in the course of winter. This is essentially the life-history as described by Ussing for material collected from a little farther north.

But when we consider the size-changes, further conclusions may be drawn. For

whereas Ussing found a size-increase only in summer, here the sizes of the various stages show an increase in both summer and winter. In the summer rise there is a slight delay between the time of appearance of the maximum size of one stage and that of the next more advanced stage. Ussing observed a lag in the increase in size from stage to stage in *Calanus*, the size-increase of the early stages developed in summer appearing as a maximum in the size of stage V in late summer, and he suggested the delay in the size-increase was such as to appear in the adult female in mid-winter, and from this he concluded the size attained by a copepod following a moult was affected by two main factors, the size preceding the moult and the nutrition at the time of moulting. His material for the adults was rather scanty, and it would appear not unlikely that this impression of the long lag between stage V and adult could be given by confusion of the summer size-increase with one occurring in winter to give the impression of a much greater lag in the appearance of maximum size than is really the case. In this material, this lag was apparently about a week per stage, and as the duration of a single copepodite stage appears to have been 3 or 4 weeks, it follows that the size attained after a given moult must depend much more on the state of nutrition in the immediate past than on the size before moulting; if not, the lag would have been greater. Indeed, from the evidence it may well be that the size of the preceding stage has no effect at all, and the lag was caused entirely by the time delay in the development from stage to stage of a batch of individuals.

The mid-winter rise in median size was symmetrical roughly about the end of January, and it occurred simultaneously in all the stages affected. It was reflected in the yearly curve of the copepod biomass given in the last paper. There was no delay in the appearance of maximum median size in one stage and in the next more advanced stage as in summer. The size-increase clearly had no immediate connexion with either phytoplankton production or temperature. The increase was due to the appearance in the nets of larger individuals, not only to the disappearance of smaller individuals, and it occurred over the same period in which the *Metridia* group appeared in the surface layers, a period suspected of being the darkest in the sea. There is clearly some relation between the capture of these large individuals and the light intensity. The size-changes over winter were probably due to differential vertical movements, the largest specimens leaving the surface first in autumn, rising last in spring, and taking part most actively in the mid-winter rise.

This presence of large individuals in mid-winter affects our interpretation of the life-history. For since these large specimens and also the adult males, which to a certain extent accompanied them, rose in late autumn and sank in early spring, they must have been present in the depths before and after the mid-winter rise. The fundamental cause of an increase in size is the presence of rich phytoplankton for, as will be described later, the summer increase was the only size-increase in the year shown by *Oithona* and by the youngest stages of the other copepods which are probably too small to be able to make vigorous vertical movements. The large winter individuals of stages IV–VI must therefore have been formed by moulting from the previous stages during the time of maximum phytoplankton—that is, in June, July and August. Some of the large members of stages IV and V may have developed from nauplii that summer, but it would appear from the abundance curves that even the earliest of the current year's

crop of nauplii could only have reached stage V, and possibly a few the adult state, at or after the end of August when the size was beginning to decline. Large individuals of stages IV and V only arose in June, July and August. Large adults may have been produced at this time below the sampling level. These individuals were those which had risen from the depths after over-wintering as younger stages. They therefore started life as the latest hatched nauplii of the previous year. These individuals therefore had a 2-year life cycle.

Whereas there is little doubt that bimodal grouping can be produced, as Ussing held, by the sudden change of the food conditions from minimal to optimal, it would appear that the bimodal groups found in the late stages of *Calanus* were in fact composed of individuals of different year-groups most of the time. Thus at the very beginning of the phytoplankton peak mainly small individuals were present. These were 1 year old, being the earlier maturing members of the previous year's crop of nauplii. The few large specimens were 2 years old. At the middle of the phytoplankton peak mainly large individuals were present together with a number of small ones. The large were mostly 1 year old, being derived from the small individuals of a few weeks previous by moulting under good conditions of phytoplankton. They were probably accompanied by a small number of individuals of similar large size which were 2 years old—the large specimens which had been encountered in winter, and which probably still survived rising above the 50 m. level somewhat later than the smaller ones. The small individuals were 1 year old. At the end of the phytoplankton peak small individuals appeared again, having developed from nauplii in the preceding 2 or 3 months. In the middle of winter the large individuals were of the order of 18 months old and the smaller of the order of 6 months old. The numerical proportions of the two size-groups may be accounted for roughly in this manner for they decrease with age. Thus at the beginning of the phytoplankton peak, the small (1 year old) individuals are much more abundant than the large (2 years old). At the middle of the peak, large and small were roughly equally numerous, the greater part of each of these groups being 1 year old. The proportion of 2-year-old large specimens would be very small. At the end of the peak, small forms were much more numerous again, being 2 or 3 months old as against 1 year for most of the large. In winter, the small (6 months old) individuals should be much more numerous than the large (18 months old), but the position was reversed by the large specimens rising to the surface selectively.

The drawback of this interpretation of the life-history is that whereas the smaller size-group of *Calanus* passed from V to the adult state, matured and laid eggs which then developed to stage IV or V by October to November, some members of stage III would be required to have developed no further than to stage IV before they sank again. This might perhaps be possible if there is a wide range in individual behaviour, these particular specimens being those which spent only a brief time at the surface, rising last and sinking first. The above interpretation of the size-groups is based on the fundamental idea that the material of *C. finmarchicus* in these waters consists of a single species. The possibility must be considered that there are two forms involved, a larger and a smaller, much as has been shown for the *Calanus* of the North Sea by Rees (1949). If this were so, the larger form might well be a hybrid between the smaller form and

C. hyperboreus. The evidence for this is that the larger form is intermediate in size, in its general appearance and in its vertical distribution in summer between the two, and that it appears in this polar water where the two groups are co-existent but not, for instance, in British waters where *C. hyperboreus* is absent. Furthermore the size-range of *C. finmarchicus* in arctic waters, considering the two groups together, is very extensive, whereas if we consider the larger and smaller forms separately over May, June and July, each group can be seen to increase in size to the extent of 12–15% of the length as does *Calanus* in the Clyde (see Marshall 1933). In *Oithona*, in which there is so far no suspicion of there being two groups, the annual variation in median size has about the same range, that is, about 10% of the total length in this case, in the two places (compare Marshall 1949, fig. 28, with Fig. 16 of this paper).

Against this possibility that *Calanus* might consist of two forms is the fact that careful examination of the individuals of the small and large size-groups (see Jespersen 1934) has failed to reveal any differences such as separate *C. finmarchicus* and *C. hyperboreus*. Furthermore if we consider the larger and smaller groups separately, the larger group had a single period of abundance in the middle of the summer and the smaller group had two periods of abundance separated by a gap. It is very difficult to see how this could come about, because if the two periods of abundance of the smaller group represented separate generations, the rate of development in summer would have to be very much faster than that of the smaller species of copepods. This is unlikely because in other waters, as here if we consider *C. finmarchicus* to consist of a single species, the rates of development of *Calanus* and of the smaller copepods are rather similar. If we considered the two periods of abundance of the smaller group as a single generation split into two parts by some factor causing the absence of the stock in the middle, we have to account for that factor, and on the whole it would seem very improbable. Thus on the basis of these size and abundance figures it would seem unlikely that the bulk of the forms referred to here as *C. finmarchicus* consist of more than a single species.

This interpretation of the life-history therefore represents to a certain extent a compromise between existing views. Adler & Jespersen (1920) considered that in Danish waters moulting at low temperatures led to a greater size than moulting at high temperatures, and Størmer (1929) associated size with temperature in West Greenland waters. It was a commonly held view that a decrease of temperature produced an increase in size. This may be so in some waters, but the present observations confirm those of Ussing (1938) in suggesting that the amount of food is of overriding importance in causing seasonal variation in size in East Greenland. The present material suggests that the two size-groups of the late stages arise in the same body of water as Ussing thought, and not in different water masses which were subsequently mixed, as was suggested by Størmer for West Greenland and by Ottestad (1932) for certain antarctic copepods which exhibited a rather similar size-variation. The life-cycle was considered to be mainly annual by Damas & Koefoed (1909), Størmer (1929), and Ussing (1938); and Størmer & Ussing thought some specimens might last a second year. Gran (1902) had concluded that some of the *Calanus* in the northern part of the Norwegian Sea took more than 1 year to come to maturity, and Ottestad (1932) considered the idea of a biennial life-history for an antarctic species of *Calanus*, although he rejected it in

favour of a theory involving mixing, like that of Størmer (1929). We conclude that the population in East Greenland is mainly annual, but that large individuals of late stages found at the surface in mid-winter are of the order of 18 months old, and probably survive 2 years.

(*b*) Calanus hyperboreus (*Table 1*)

Although less common than *C. finmarchicus* the periods of abundance (Fig. 1) were somewhat similar. The bulk of the stock was doubtless below the 50 m. level and a proportion of those in the surface layers no doubt escaped the net. The nauplii and

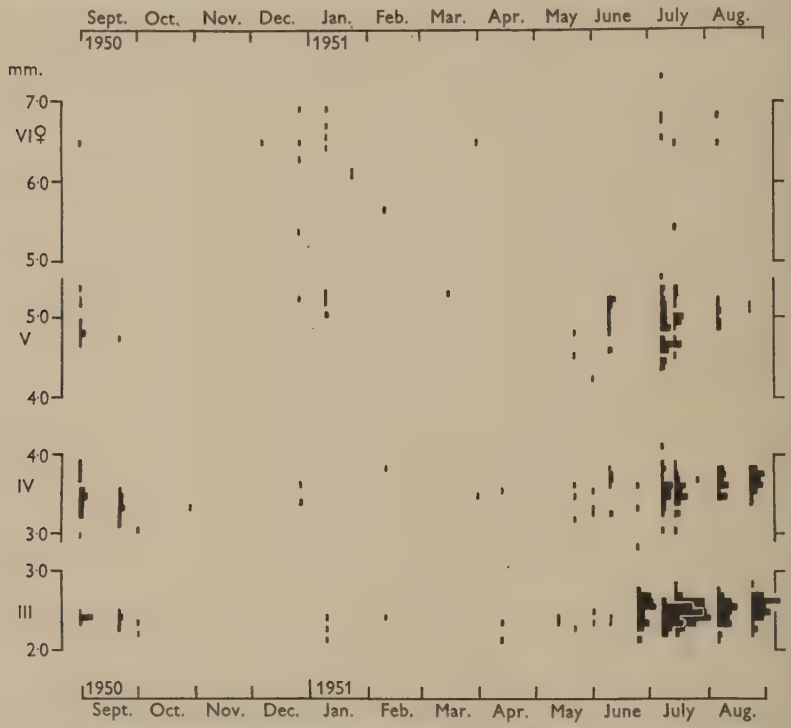

Fig. 3. *Calanus hyperboreus*, size-groups of stages III–VI. (Stages I and II are included with *C. finmarchicus* in Fig. 2.)

stage I have been included with *C. finmarchicus*. Stage II was abundant in June–July–August, the period of maximum abundance having thus been 6 weeks or so earlier than in *C. finmarchicus* and much shorter in duration. Stages III and IV were abundant from July to September, and stage V from June to August. Adult females were taken occasionally in the summer period and in mid-winter. No adult males were caught.

The seasonal changes in size (Fig. 3) appear to have been comparatively slight, but the species was not taken in sufficient numbers in winter to be sure. Unlike *C. finmarchicus*, the late stages gave unimodal size-groups but their scatter, although based on so few specimens, suggests a similar appearance of larger specimens in mid-winter.

Following copepodite stage II back in the abundance graph it can be seen that these individuals had probably arisen from the earlier, April to June, members of the

combined group of *Calanus* nauplii. The abundance graphs show only a suspicion of the rising of the late stages of the breeding stock to the surface in early summer before the production of these nauplii set in, but this may just have been due to the scarcity of the species in the surface layers. Stage II can be seen in Fig. 1 to have developed to stage III, but further development was obscured to a larger extent than in *C. finmarchicus*, by the stock disappearing, probably by sinking to the depths. Late stages, however, were taken in the surface layers during the winter months, an obvious parallel to the state of affairs in *C. finmarchicus*. As the production of nauplii, as shown by the time of appearance of stage II copepodites, was some 6 weeks earlier than in *C. finmarchicus*, it probably indicates that the whole stock of *C. hyperboreus* rose from the depths earlier than *C. finmarchicus* in these Greenland waters, as is known to be the case in Norwegian waters (Sømme 1934). This early breeding would probably enable the nauplii produced in summer to reach later stages of development that summer than in *C. finmarchicus*, but so few were taken in winter that we have no evidence for this. On rising next spring as stages III–VI, the stock of *C. hyperboreus* by virtue of its early start would be likely to achieve maturity more completely than the stock of *C. finmarchicus*. Now *C. finmarchicus* shows a great size-range with the production of bimodal groups in the later stage, and we are in agreement with Ussing (1938) in considering these to be due to growth under different phytoplankton conditions. If this is so, the unimodal groups of *C. hyperboreus* probably indicate that all the stock matured under uniform phytoplankton conditions. Quite possibly all the stock became mature during the first summer after the summer in which the eggs hatched. Ussing (1938) observed the same early spawning and concluded on the abundance figures that there was a 1 year life-cycle. It is probable that the bulk of the large specimens of late stages caught in mid-winter were only 6 months old at the time, but there is a possibility that some of them might have been 18 months old as in *C. finmarchicus*. For it is only the size distribution which reveals to us that some specimens of *C. finmarchicus* have a 2-year life-cycle, and in *C. hyperboreus* size gives us no evidence.

(*c*) Pseudocalanus minutus (*Table 2*)

Nauplii were present (Fig. 4) all the year round, abundant from May to November with a maximum in June and July and a minimum from December to March. Copepodites I–V were present all the year round, stage I having its maximum from June to November and its minimum in April and May, and the position of the maxima and minima occurring later in successive stages so that stage V had its maximum from September to November and its minimum in July and August. Adult females were present throughout the year with a maximum from April to August. Males although scarce were at their maximum from May to July corresponding to the summer increase of adult females.

As in *Calanus* there were two periods of increase in size (Figs. 5, 16). The summer increase was marked in stages I–V and was just noticeable in the adult females, and there was very little lag, if any, between the time of development of maximum size in one stage and in the next. The winter increase, present in stages IV and V and suggested in stage III, was symmetrical about the end of January as in *C. finmarchicus*, although it was much less evident than in this latter species. It appears that the size of the adult

females was increased in November and December by some factor other than the immediate presence of phytoplankton or the mid-winter rise. The males of stages IV and V were somewhat smaller than the corresponding females for most of the year, and the adult males, over the period from April to June when they were abundant, were considerably smaller than the adult females. The adult females in summer did not exhibit a fully bimodal group as in *C. finmarchicus*, but a unimodal group of small individuals with a long tail of individuals of larger size. Size-groups of stages I–V were all unimodal.

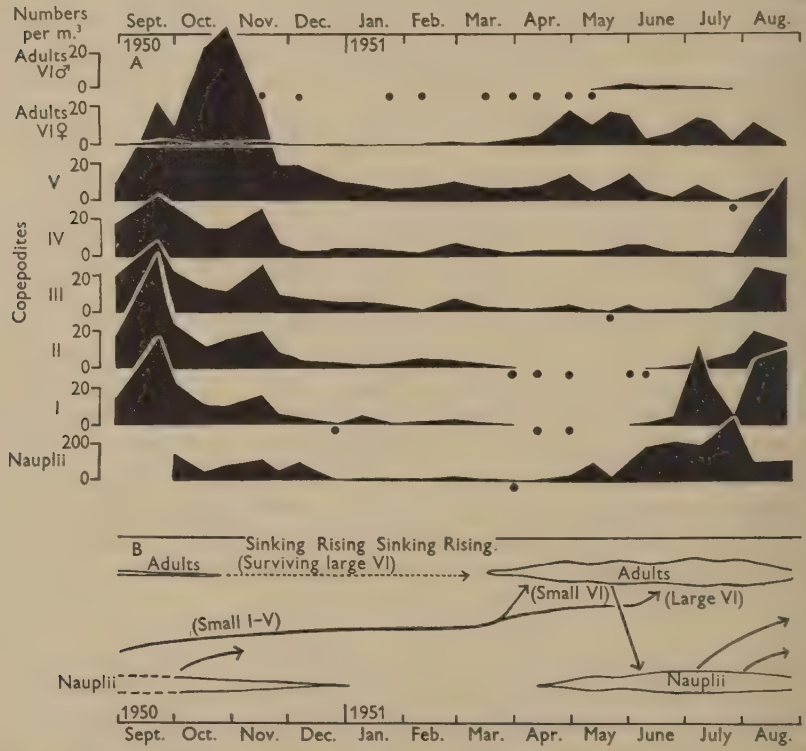

Fig. 4. *Pseudocalanus minutus*. A, abundance: scale of nauplii one-tenth that of remaining stages. Dots indicate specimens present in small numbers, nauplii below 5·0 m.³, stages I–VI below 0·5 m.³. B, interpretation.

As in *Calanus*, the spring increase of the later stages in March, April and May was not preceded by nauplii and copepodites of stages I and II and was therefore first caused by the rising of the later stage from the depths. In this case, these upward migrating late stages were almost entirely adult females, together with a few adult males and very few stage IV and V copepodites, for all the stages of copepodites up to and including stage V showed only a slow decline in population from November until the appearance of the new generation in June, July or August according to the stage. Adults present from the period April to November gave rise to the contemporaneous

group of nauplii, the June members of which developed to stage V by September, the later hatched members reaching intermediate stages by that time. A few individuals may have reached the adult state between September and November and may have

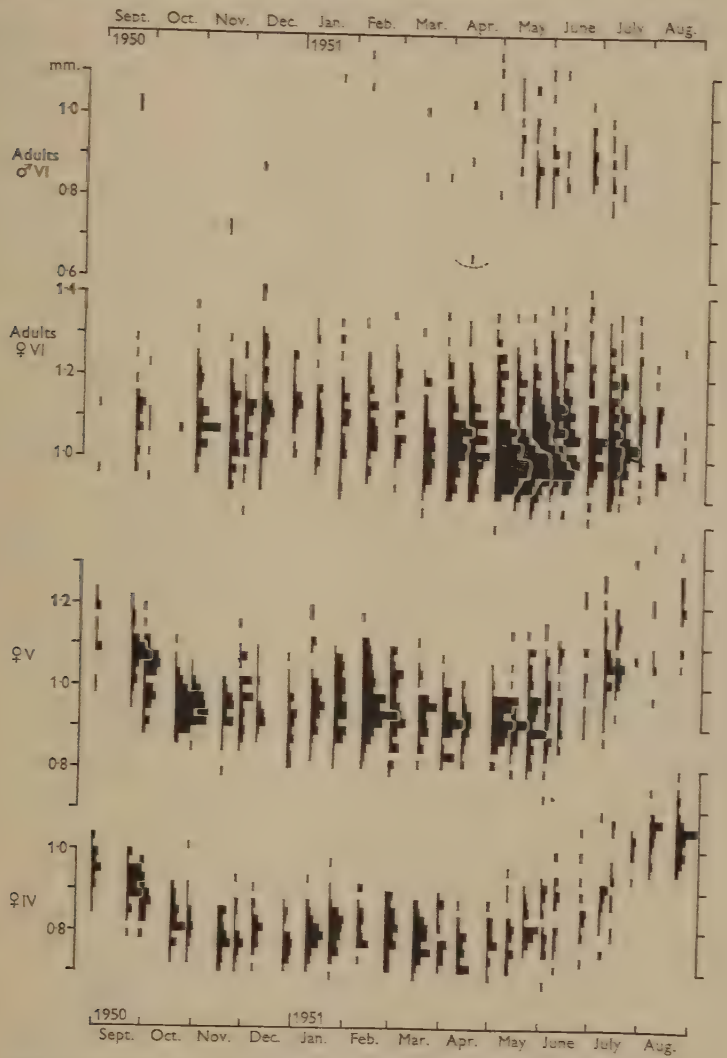

Fig. 5. *Pseudocalanus minutus*, size-groups of stages IV ♀, V ♀, VI ♀ and VI ♂.

been responsible for the nauplii appearing at this time, thus running through the whole life-cycle in one summer. Development of these nauplii, however, was uncertain. Whether the small numbers of nauplii and of stages I and II which were found throughout winter were being produced at that time and were actually developing, or whether they survived without change from autumn, their growth arrested by lack of food, we

cannot say. The productive brood of nauplii, however, was that produced the following summer from eggs laid by females which rose in early summer as adults. These may have moulted from stage V any time between autumn and their appearance in early summer.

The size-changes are traceable to the increase or decrease in size consequent on moulting in periods of good or poor phytoplankton and to the effect of the mid-winter rise of large specimens as discussed under *Calanus*. The presence of large adult females in October and November probably does not mean that they moulted at this time with a lag in size consequent on their having developed from large stage V, but that they were formed below the surface in summer and rose at this time for egg-laying. There was only a small amount of lag, if any, found between the time of attainment of maximum size in successive stages from stages I to V (Fig. 16), and as in *Calanus* this supports the view put forward in this paper that the size attained following a moult is almost wholly dependent upon the state of nutrition at the time of moulting and there is little, if any, carry-over of large size from stage to stage. The winter size-increase which affected stages IV and V and the adults was much less marked than in *Calanus*. It was centred about the end of January in exactly the same way. In the case of the adult female the winter size-increase would appear to have been masked by being merged with a size-increase enduring from late autumn, probably due to the presence of mature females in the upper water layers for egg-laying. As in *Calanus*, Ussing (1938) described the summer size-increase but not that of winter.

In summer the adult females did not form a bimodal group as in *C. finmarchicus*, but a unimodal group with a long 'tail' of individuals of larger size. It seems probable that the large group of smaller individuals were those which moulted from stage V during the previous autumn or winter and the 'tail' of large individuals were those which partook in the spring rise as stage V and moulted to the adult state in summer under conditions of abundant phytoplankton. It is possible that the large individuals arose as the earliest members of the autumn brood, completing their development before the phytoplankton declined, but this seems less likely. As in *Calanus*, therefore, the capture of large individuals of late stages in mid-winter has to be explained. Larger winter members of stages III–V may well have arisen by the earliest members of the autumn brood moulting under good phytoplankton conditions, but it would appear that very few reached the adult state before the phytoplankton had declined. Quite possibly, therefore, the large adults found in mid-winter arose from the previous generation, that is, from the small number of nauplii and young stages found the winter before. As these large adults occurred in mid-winter they probably contributed to the increase in both size and numbers during the rise to the surface at the beginning of summer. Thus it seems most likely that although most of the stock passed through one generation in the year, a few individuals may have passed from egg to adult in one summer season and a part of the population probably had a $1\frac{1}{2}$-year life-cycle. The main size-group of adults with its 'tail' of larger individuals are the counterpart of the two modes in the size-groups of *C. finmarchicus*, the larger group in each case being composed of specimens older than those of the smaller group. Ussing (1938) considered the life-cycle to be almost entirely annual, although possibly a few individuals might pass through all stages in one summer.

The rate of development of the stock in summer as seen from the abundance graphs appears to have been: adults to nauplii, possibly 2–3 weeks; nauplii to copepodite V, 30 June to 30 October, 16 weeks; copepodites III to adults, 30 April to 30 July, 13 weeks. Thus, had the phytoplankton conditions been suitable over a longer period the development from adult to adult would have taken about 20 weeks as in *Calanus*. Development in winter is uncertain.

(*d*) Oithona similis (*Table 3*)

On the whole the summer to winter differences in abundance were much less than in the other species. Eggs were abundant (Fig. 6) from June to October and were virtually absent from December to March; their minimum appeared to be in January

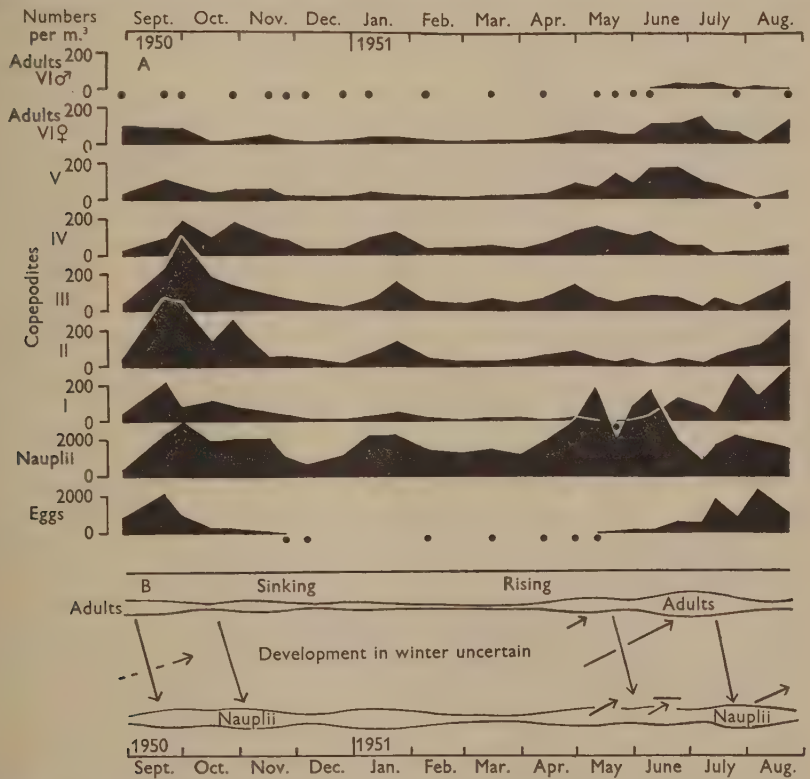

Fig. 6. *Oithona similis*. A, abundance: scale of eggs and nauplii one-tenth that of stages I–VI. Dots indicate specimens present in small numbers, eggs below 50, late stages below 5·0/m.³. B, interpretation.

and February. Nauplii and all copepodite stages were present throughout the year. The nauplii had a period of abundance in May and June, were less abundant in July and August and were more abundant again from September to November. They also showed a period of abundance in January, together with young copepodite stages. The numbers of copepodites and adults showed a slight overall decline over winter.

Copepodites I–III showed successive maxima respectively in the periods from June to October, July to November and August to November, with minima in May–July. All showed an increase in January, and stages II and III showed increases in April and May. Stages IV, V and the adult females each showed two maxima in summer, separated by a gap; stage IV having its maxima from April to June and from August to November, stage V and the adults from April to July and from August to November, the peaks in the adults being possibly a little later than in the stage V. Adult males were present throughout the year, but were most abundant from June to August.

All stages increased in size over summer (Figs. 7, 16) and there was very little lag between the times of maximum median size in successive stages. The median size of the late stages showed just a suggestion of the winter rise so prominent in *Calanus* in that while the younger stages showed a decrease in size over winter the mean size of stage V and the adult female was roughly uniform from November to April as if a normal size decrease might have been offset by a slight amount of upward movement of large individuals, just enough to keep the size uniform. All size-groups were unimodal.

As in *Calanus*, from the fact that the increase became evident in all the late stages at about the same time, we may conclude that the spring increase was a result of an upward movement of the stock from below the 50 m. level and it was followed, or accompanied by, the maturing of stages III–V. Stage IV, present from April to June, developed to stage V from May to July and to the adult from June to August. This development of the individuals which partook in the spring rise was continuous with the development of those which probably arose from nauplii and stage I in March, where however no peak of nauplii showed in the abundance graph, to adults in July. The long period of abundance of nauplii over summer from April to November, while split into minor peaks as nauplii, was derived from a single period of abundance of eggs. There was no obvious relationship between the nauplii peaks in summer and the peaks of later copepodites. It seems probable that this was owing to grazing by the large *Calanus*, as was suggested by Ussing as being the reason for the paucity of *Oithona* nauplii in summer. It may be that this grazing effect was not noticeable in the egg abundance because perhaps at that time most of the egg-masses were attached to the adult females in the sea and would thus have been less affected by grazing. Only on three occasions were more egg-masses recorded than could be carried at the rate of two per female. A depression in the number of stage I in May and stage II in June, probably due to grazing, appears to have been carried on to stages III and IV in July and to V and the adult females in early August. The increase in stage I from June to August, marking the new generation, can be seen to have arisen by development of nauplii present from late May onwards. Some of these probably arose from individuals which had over-wintered as stage V or as adults while some possibly developed from those which had been present as nauplii in March or April. These stage I copepodites present from June to August probably became adult some time after August 1951. Referring back to the beginning of the graphs, that is, to autumn 1950, a group of stages I and II which were abundant from September to October and which were probably the other half of the peak seen in July and August 1951, give an impression of having developed to adults in the period October to December in the face of the

overall decline in the stock, although this is not at all clear. Thus there appears to have been mainly one generation in the year, effectively cut into two groups by some factor, probably predation by *Calanus* which caused mortality to nauplii and stages I and II in June, while some individuals probably passed through two generations.

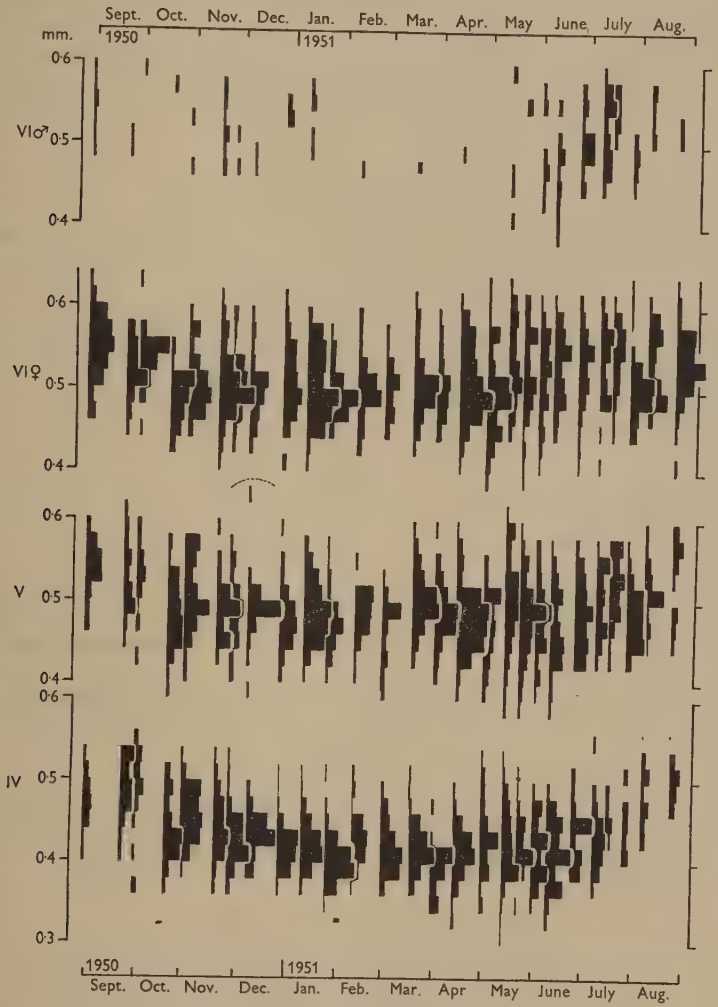

Fig. 7. *Oithona similis*, size-groups of stages IV, V, VI♀ and VI♂.

Ussing (1938) found the species to reproduce at all seasons, the number of eggs increasing at the beginning of summer but the most productive brood of nauplii being that of September–October. He considered the species not to belong to the group with a summer increase. In this paper it is held that it does belong to the group with a summer increase (see seasonal distribution of eggs, Table 3). It is, however, present

throughout winter to a greater degree than are the other 'summer' species and it does appear that, as Ussing pointed out, it suffers greatly from grazing by *Calanus* in summer.

The rates of development that may be estimated from Fig. 6 are: copepodites II to adults, 1 May to 1 July, 8 weeks; copepodites II–IV, 1 July to mid-August, 6 weeks. Eggs to copepodites II probably takes 6 weeks. Thus had the phytoplankton conditions been suitable over a longer period, and were a new batch of eggs to follow a group of adults in 2 or 3 weeks, the development time per generation, adult to adult, would appear to have been 16–17 weeks.

(*e*) Oncaea borealis (*Table 4*)

The assessment of the numbers of *Oncaea borealis* was often a little troublesome because the species, although quite numerous, is of such a size that it is difficult to separate it from the phytoplankton. For this reason the abundance figures have been based on counts of rather few specimens.

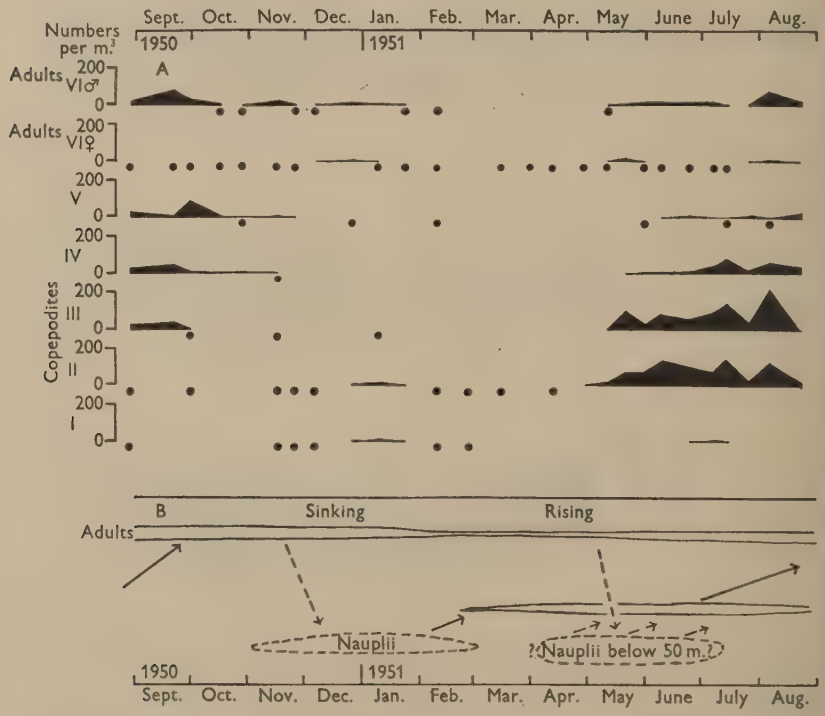

Fig. 8. *Oncaea borealis*. A, abundance: dots indicate specimens present in small numbers below 5·0/m.³. B, interpretation.

Oncaea was taken throughout the year (Fig. 8). Eggs were found in some numbers. Nauplii which might be assigned to this species were very likely included with the much more numerous *Oithona* nauplii, but the copepodite stage I, which is easily recognizable and quite distinct from that of *Oithona*, was very scarce. As there is no

particular reason for supposing these stages were of very short duration, they were probably passed through below the 50 m. level. The line of development of copepodite stage II of May to August to stage V of June to November is very clear. Although there was no obvious peak of adult females at any time of the year the occurrence of the males from May through summer to January with a peak in August and September suggests that stage II of one summer may have developed as far as the adult that same summer or autumn. Subsequent egg-laying might have been responsible for the occurrence of stage I in the period November to February. Whether stage II developed directly from stage I in winter and the population of stage II rose to above the 50 m. level in May to give the period of abundance which started from then, or whether the winter stage I developed no further or died and the summer group of stage II was part of a population which began its development as nauplii from April to June below the 50 m. level, or again whether the nauplii and stage I were passed through outside the fiord and the stock subsequently came in with the current we cannot say. Were a single whole generation from egg to adult to be passed through in summer and autumn, the development time for a generation would have been roughly 20 weeks. Ussing (1938) found *Oncaea* to be much more abundant in summer,

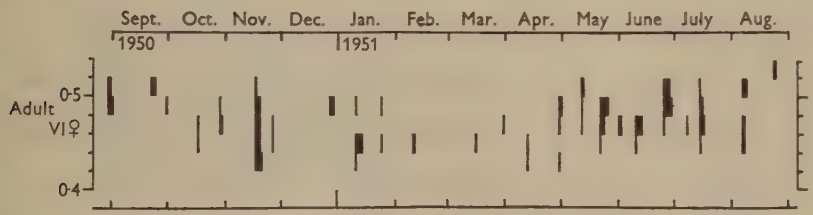

Fig. 9. *Oncaea borealis*, size-groups of stage VI♀.

during which a new generation was developing, the winter population being small and composed mainly of adults. He considered the chief spawning time to be April and May, but his account does not give us any further information on the puzzling discontinuity in abundance between stages I and II.

Although few specimens were measured, the size of the adult females (Fig. 9) suggested an increase in summer and again in mid-winter with the largest decrease in March, much as in the other species.

(*f*) Microcalanus pygmaeus (*Table 5*)

All the *Microcalanus* material taken at Scoresby Sound is considered to belong to this species. Specimens of *Microcalanus* collected north of the New Siberian Islands by the 'Fram' expedition were described by Sars (1900) as *Microcalanus pygmaeus* G. O. Sars. It is distinguishable from the Norwegian *M. pusillus* (G. O. Sars) (Sars 1903) in having somewhat larger antennules and being of rather larger size. With (1915) considered the two to be forms of the same species, but Farran (1936*a*) in reporting on the 'Nautilus' collections from Spitsbergen waters drew attention to the existence of both forms in the hauls. Ussing (1938) found the size of thirty-eight adult females of *Microcalanus* to form a bimodal group, and suggested the variation in size

to be similar to that in *Calanus*, and again Jespersen (1939*a*, *b*) made no distinction between the two forms, grouping them as *M. pygmaeus*.

Ussing found *Microcalanus* at the surface in winter, and concluded that the stock sank below the 50 m. level in summer, exhibiting a different pattern of behaviour to that of *Calanus*. The material at his disposal, although rather scarce, suggested spawning from January to March, on the strength of a greater proportion of females to other stages and on the presence of a number of small nauplii in the samples at this time. He considered it questionable that the main spawning could occur at this early date, suggesting it more likely to be somewhat later, in early summer.

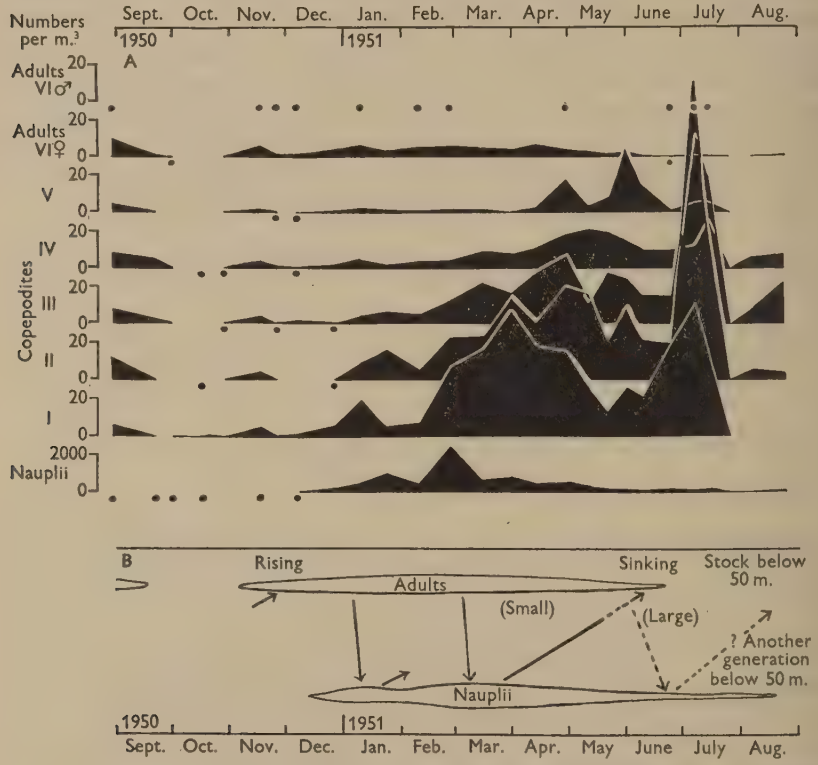

Fig. 10. *Microcalanus pygmaeus*. A, abundance: scale of nauplii one-hundredth that of remaining stages. Dots indicate specimens present in small numbers, nauplii below 50/m.³, copepodites and adults below 0·5/m.³. B, interpretation.

In this Scoresby Sound material copepodites and adults were most common in the surface layers over the spring and early summer months. Nauplii were found mainly from December until August, the main peak being in the period from January to March, confirming Ussing's observations. These nauplii developed through the copepodite stages at progressively later dates, reaching stage V from April to June. In the abundance graph (Fig. 10) stage V cannot be seen to develop into adults as these latter did not appear at the surface until winter. The size-distribution of the winter females,

however, suggests that many were formed in summer. At this time the bulk of the stock was below the 50 m. level, and if some females became mature in the summer below the 50 m. level it seems not impossible that they may have laid eggs then and there in the depths and the winter breeding seen in the surface waters may be only a part of the tale. There was a sharp peak of stages I–IV in June and July, suggestive of the young stages of a new generation. These did not however develop to later stages, at that position at any rate, and their appearance may have been in the nature of an artifact caused by water movements.

The size-distribution of the specimens caught by the fine net, that is, of the individuals from which the abundance figures (Fig. 10) were taken, is depicted in Fig. 11 in the form of a series of solid histograms. In addition to the specimens caught in the fine net, a number of stage V and adults, of large size, were taken in the coarse net. This net fished a much greater quantity of water, and in this case the smaller individuals of these stages were lost from the sample by slipping through the meshes. These larger specimens from the coarse net have been added to the size-groups of the fine net material as histograms bounded by broken lines. It should be noted that owing to the method of construction of this figure the diagrams for stages V and the adults may not necessarily indicate a real bimodal size-distribution; they probably indicate a peak with an extended 'tail' of larger individuals rather like *Pseudocalanus*. The larger sizes of each stage, although they appeared at the same time in April and May, disappeared serially; thus the larger sizes of stages I–III were restricted to the period from May to September, and stages IV and V from May to January. There was a period from August to November when the stock was scarce in the surface layers. Adult females of large size were present over the winter months and survived at any rate until May. Nearly all the adult males, the bulk of which occurred from November to February, were large specimens. In the other species it has been shown that large specimens arose only in summer and that there was very little carry-over of a large size through moults in winter. It therefore seems probable that all the males and some of the females were formed in summer, and since they were not at the surface at this time they were probably down below the 50 m. level, and their appearance at the surface in winter represents simply their time of movement to the surface. The formation of the 'tail' of large individuals in the size-groups of later stages in *Microcalanus* is therefore not quite comparable to the formation of bimodal groups in *Calanus*, and the 'tail' in *Pseudocalanus* in that it is definitely not caused by some of the individuals lasting 2 years. *Microcalanus* therefore passed through one generation a year at the surface, and this seems to have taken about 25 weeks from nauplius to adult, rather longer than in the summer breeding species as might be expected. Although its size is obviously affected by the presence of phytoplankton, the stock develops in the early months of the year in its complete absence.

(*g*) Metridia longa (*Table 6*)

All stages of this species were more common in the surface layers in winter than in summer (Fig. 12), as noted by Ussing (1938). Comparatively few specimens were caught but they were sufficient to show the main trends in the life-history. Compared with the number of later stages, comparatively few specimens of stage I were taken.

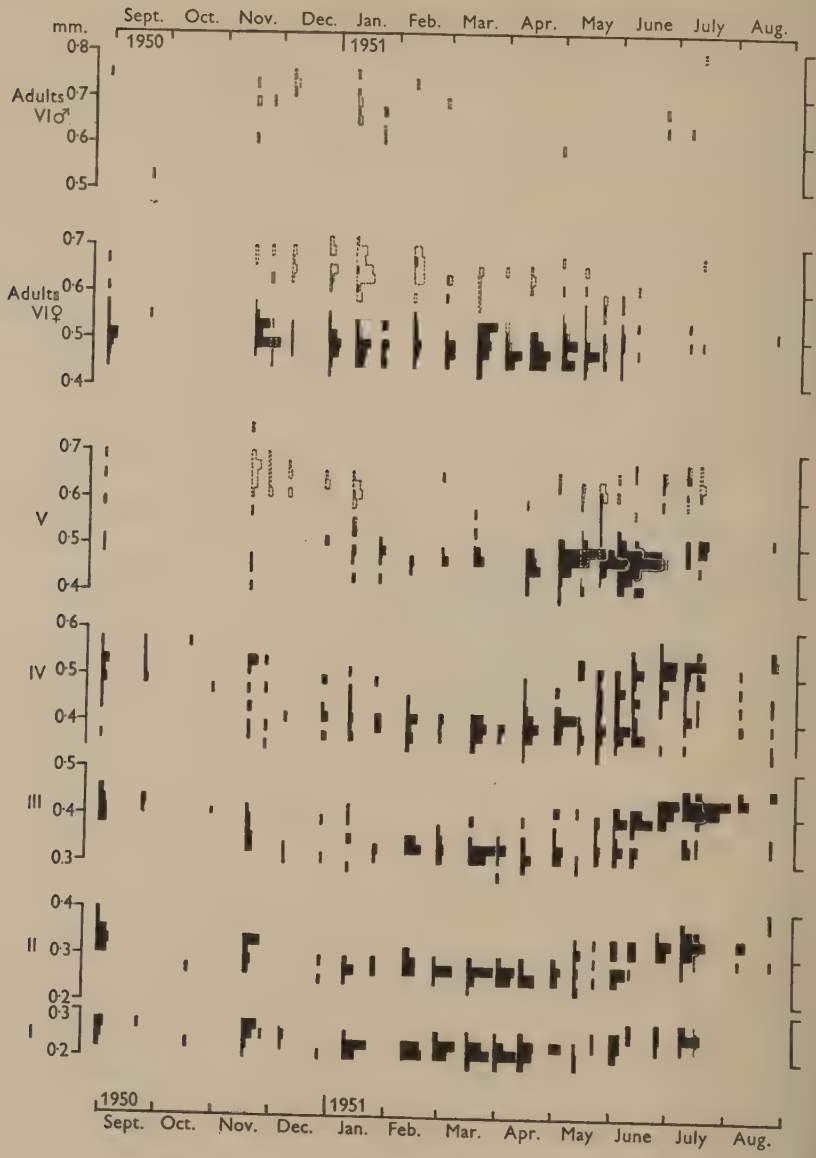

Fig. 11. *Microcalanus pygmaeus*, size-groups of stages I–V, VI ♀ and VI ♂. Solid histograms represent specimens taken in a fine net; histograms bounded by broken lines represent specimens taken in a coarse net, from which smaller individuals were lost by escape through the meshes.

This suggests the production of nauplii occurred below the upper 50 m. of water fished by the nets. No nauplii were identified as such, but the few that may have been encountered would have been included with *Calanus* or *Pseudocalanus*. Development is not at all clear, but if we may connect the graphs of the latter part of 1951 with the earlier part of 1950, we may suggest a line of development from an extended period of abundance of stage I from May through summer and autumn until January, to an

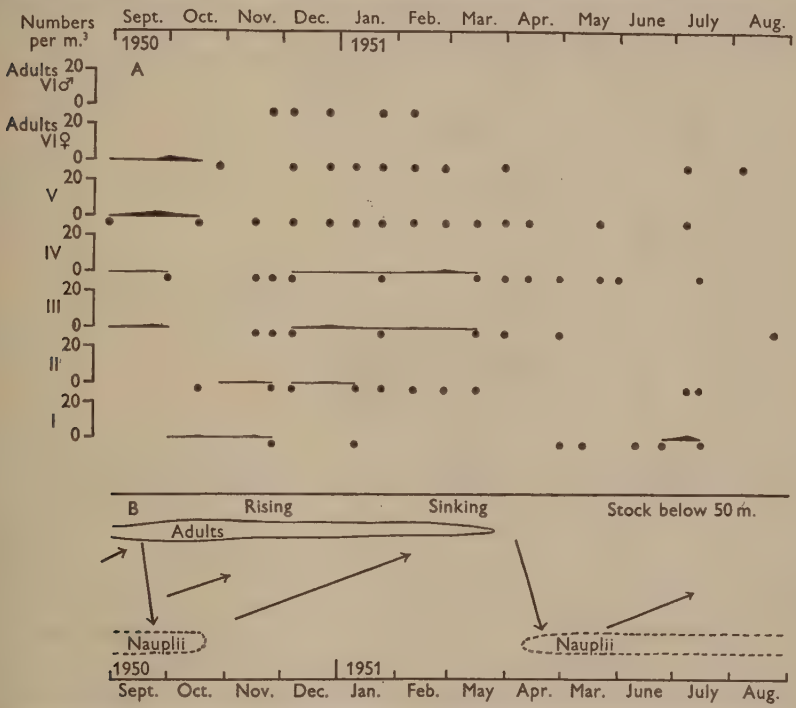

Fig. 12. *Metridia longa*. A, abundance: dots indicate specimens present in small numbers below 0·5/m.³. B, interpretation.

extended period of stage IV, found most of the year with a maximum from November to March. That is, the development from stage I to IV took about 6 months. Development from then on is probably obscured by the vertical movements, towards the surface in late autumn and away from it in early spring. It would, however, seem most likely from the development of stages I to IV in winter and the presence of stage I from May until July, that adults have been produced in greatest abundance from perhaps February to July, mostly below the 50 m. level. The autumn and winter occurrence of adults at the surface was the result partly of their season of abundance and partly of their upward movement in winter. Similarly, the capture of adult males only in mid-winter probably represents not their true period of abundance but simply their time of visiting the upper layers. Ussing (1938) considered the eggs were laid in August–September, and he found the new generation developing in winter. I consider the breeding season to have a greater spread. The likelihood of summer

breeding in the depths is heightened by the figure given by Bogorov (1946*a*) for the percentage composition of the *Metridia* stock from the 'Sedov' drift in the Arctic Ocean from 1937 to 1939, for this shows a distribution of stages from the copepodite stage I to the adult during summer much as in *Calanus*.

The size of stage V and of the adult females showed little variation during the period from October to March when they were common at the surface (Fig. 13). Ussing noticed this uniformity of size and attributed it to moulting taking place outside the period of phytoplankton abundance. In the Scoresby Sound material, however, it seems likely that development went on in the depths during the summer at a time

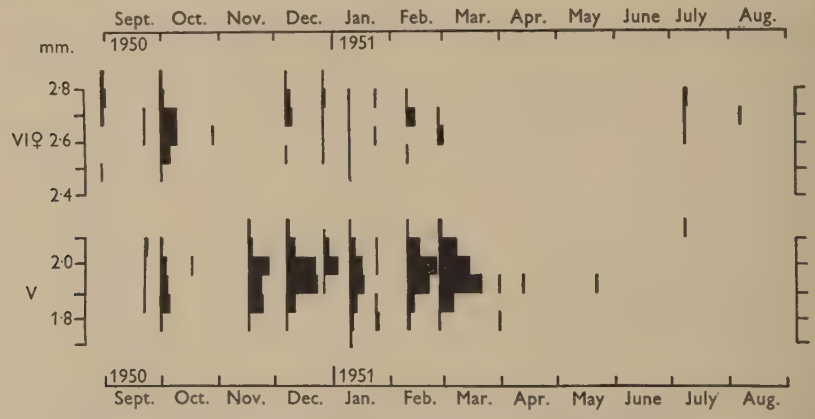

Fig. 13. *Metridia longa*, size-groups of stages V and VI♀.

when moulting in the other species gave rise to an increase in size. The feeding conditions are, of course, more uniform in deeper water, but a uniform size might arise from other reasons. Since the species avoids the surface with its high phytoplankton density in summer and can, like *Microcalanus*, develop through its various stages in winter it is clearly not so dependent on the phytoplankton as for instance is *Calanus*, and it may lack the ability to assimilate food much faster in summer than in winter. Its uniformity of size may be the result of its vertical distribution and feeding habits.

(*h*) Pareuchaeta *spp.* (*Fig. 14, Table 7*)

Two species, *Pareuchaeta norvegica* and *P. glacialis* are found in these regions. Some 120 immature stages belonging probably to one or the other, or perhaps to both of these species, were encountered in the samples.

Like *Oncaea*, stage I was scarcer than the later stages, giving the impression that the bulk of the breeding had occurred in the depths, copepodites appearing in the upper 50 m. some time later by active movement during winter. If nauplii were taken they were probably confused with those of *Calanus*, but the scarcity of stage I indicates very few, if any, would have been encountered. The pattern of the distribution of stages was somewhat similar to that of *Metridia*, but suggested a rather later breeding season. Nauplii and copepodite stage I were probably produced in the depths from about September to March. Copepodites and adults moved towards the surface in

winter and away from the surface again in the spring, stage I being least mobile and appearing in small numbers, stages II–IV appearing more commonly, and later stages appearing less commonly again, either because they spend less time at the surface or else because they escape the nets in the light period. A certain amount of development of the stock went on during its sojourn at the surface in winter, but the main part of the development from stage III to adults occurred below the 50 m. level, adults probably being produced some time in summer.

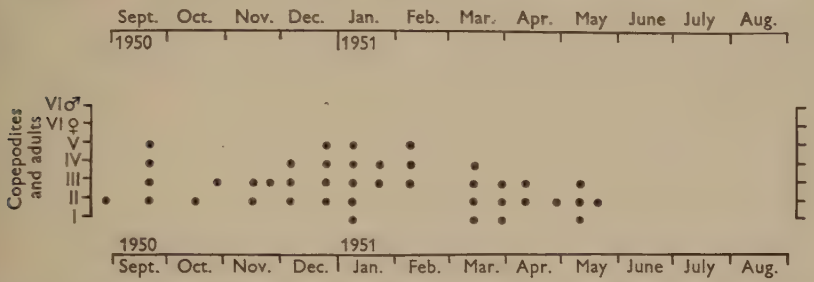

Fig. 14. *Pareuchaeta* spp. Abundance; dots indicate specimens present in small numbers 0·5/m.³.

(*i*) *Other species*

A few species appeared in the catches as occasional specimens only, in numbers insufficient for conclusions to be drawn regarding their life-histories. They were:

Bradyetes brevis, 65 specimens. This form was described by Farran (1936*b*) from a single adult female found by Ussing (1938) in the material taken at Ella Island in October 1932. I am grateful to Dr J. P. Harding for referring specimens taken in these hauls to this species. There were two periods of occurrence, mid-winter and summer. Those appearing in the period from November to January consisted mainly of adults with a few stages III and V; the stock which appeared in summer included all the stages I–VI with the exception of the adult male. It may be suspected that the appearance of the later stages at the surface in mid-winter was due to upward movement as in the *Metridia* group, and that younger stages were produced in summer when most of the stock was below the 50 m. level.

Acartia longiremis, 7 specimens (1 stage III, 2 stage V, 2 stage VI ♀ and 2 VI ♂). Three of the specimens were dead, the body contents being partly disintegrated.

Heterorhabdus norvegicus, 2 specimens (1 stage IV, 1 stage VI ♀).

Oithona atlantica, 32 specimens (2 stage V and 30 stage VI ♀). Apparently not breeding because no younger stages were encountered.

O. nana, 3 specimens (2 stage IV, 1 stage V).

Oncaea minuta, 2 specimens (1 stage III, and 1 stage VI ♂).

In addition to the above, the two harpacticids *Microsetella norvegica* and *Ectinosoma* sp. occurred in the samples, the former throughout the year, the latter only in June, July and August. They were present almost entirely as adults and late stages; the younger stages were probably passed through on the bottom. Their total abundance ranged up to about 20/m.³, but as they came through into the phytoplankton fraction of the samples they were difficult to count and were not assessed quantitatively.

DISCUSSION

As these Scoresby Sound samples were taken only in the upper 50 m. of the water column at a fixed station, there are likely to be complicating factors, as discussed in the last paper. Thus there is a movement of the water down the coast all the while in such a way that some of the specimens taken in summer may have been produced in the region of the north pole the previous year and some may have been resident in the fiord all winter. Compared with the stations from which the material dealt with by Ussing was taken, Rosenvinge Bay in Scoresby Sound is less affected by run-off than is Ella Island in the Franz Joseph Fiord, as is evidenced by the way in which Scoresby Sound has a great deal of sea ice in summer while Ella Island is comparatively free, and it is more comparable to the Eskimonaes station on Clavering Island, out on the coast. It would seem possible that forms like *Calanus* undergo a seasonal circulation similar to that described by Sømme (1934) for the coast of Norway and by Mackintosh (1937) for the Antarctic. That is, adults taken off-shore and southwards by the run-off and by the general set of the current may sink and be carried northwards and inwards towards the coast again by the northward moving Atlantic water layer and by the counter current to the run-off so that they appear in the fiords again in the spring. Such a movement is not essential for the maintenance of a breeding stock in the surface layers of polar water, for Shirshov (1938) and Bogorov (1946*a*) found the copepods breeding in summer under the ice of the Polar Ocean. Conclusions drawn in this paper are based on the assumption that the effects of water movements are insignificant compared with seasonal changes, and that the changes at the fixed station in Rosenvinge Bay would be more or less similar to those occurring at a number of other fixed stations in polar water.

Although most of the species did not appear to run through a complete generation in summer it would appear that if the phytoplankton lasted long enough to enable them to do so they would take between 16 and 20 weeks. *Microcalanus* and *Metridia* which can develop through winter would appear to take longer. This development time may be compared with the 6–8 weeks for *Pseudocalanus* and *Oithona* in the English Channel (Digby 1950) and in the Gulf of Maine (Fish 1936*b*, *c*). Thus if we suppose that above a certain density of phytoplankton the development rate depends on the temperature, the slow development of the copepods in Greenland waters compared with that in water some 10° C. warmer indicates that they are not particularly adapted to living in cold seas.

(*a*) *Survival and growth in winter*

The survival and growth of nauplii and young stages, particularly of *Microcalanus* in winter, would be easily understood in the English Channel where the phytoplankton, measured as pigment, at no time sinks below 1 unit of plant pigment m.^{3} (Harvey, Cooper, Lebour & Russell 1935, Harvey 1950). But in Greenland, where values below 1 unit/m.^{3} are found throughout the greater part of the year beneath the ice, although *Calanus* and *Pseudocalanus* survive but only pass through one or two stages, *Microcalanus* at any rate passes through several. While a possible reduction in metabolic rate during a period of starvation might account for survival, as suggested by Ussing

(1938), it cannot account for the growth of an individual over several stages involving a considerable increase in mass. The net plankton is poor in winter, and occasional water samples examined in winter revealed no large population of flagellates nor even a great abundance of detritus which might be available as food. And indeed the water was very transparent in winter. The volume of water which a copepod can clear of fine, particulate matter in a given time is fairly small and is independent of the concentration of the food (Fuller & Clarke 1936, Lucas 1936, Fuller 1937, Harvey 1937, Gauld 1951). This filter-feeding method would provide a totally inadequate amount of food under winter conditions in Scoresby Sound, were phytoplankton the only food and were the cells distributed at random. Certainly in *Microcalanus*, if not in the other species as well, some form of feeding must go on. It is notable that although *Microcalanus* breeds and develops in winter, outside the period of phytoplankton production, as indeed it does to a certain extent in Loch Striven (Marshall 1949), the size graphs indicate that in Scoresby Sound winter is a lean period for the species. It would therefore seem at first sight that it cannot behave like *Calanus* in which egg-laying is largely dependent on the food available (Marshall & Orr 1952). *Microcalanus* has not obviously raptorial mouthparts, and therefore these do not appear to be necessary for a method of feeding which must in effect be carnivorous in the long run, whatever size particle is ingested. Since such a method of feeding must occur in *Microcalanus* it very likely occurs in the other apparent filter feeders as well, and may thus enable such a zooplankton population to maintain itself on its own reserves down to low population densities, as suggested in the last paper (Digby 1953). Ussing (1938) dissected a number of *Calanus* taken in winter in East Greenland waters and found the gut quite empty, but it may be that even in this species which, although it survives through winter, does not grow very much, a certain amount of feeding goes on. This may be sufficient for metabolic processes and perhaps one moult, and may occur at intervals of time followed by rapid voiding of the indigestible remains so that for most of the time the gut is empty.

How is this feeding effected? On the one hand, it might be by direct predation. Experiments on selective feeding carried out by Harvey (1937) for *Calanus* indicate the effective volume of water filtered is much greater when they are feeding on large particles than it is when they are feeding on small particles. We know that in summer the small stages are taken as food by the larger stages of *Calanus* (Lebour 1922, Marshall 1923, Moore 1931, Lowndes 1935) and by other species as well (Marshall 1949). These small stages no doubt serve as an intermediate step in the food chain between on the one hand, flagellates and very small particles of bacteria-laden debris and, on the other hand, the larger copepods with filtering apparatus embodying apertures of such a size as to let these particles pass through. Such selective feeding on large particles may be the normal way of feeding by *Calanus* in winter and it may be more marked in *Microcalanus* which breeds during the winter months. It is of course the normal method of feeding for the more obviously carnivorous species that live in the depths.

On the other hand, there might be filter feeding at the normal rate such as is found in laboratory experiments, restricted to the vicinity of clumps of fine particles. For small organisms such as flagellates, feeding on decaying organic matter, may well be

aggregated into clumps in the vicinity of the decaying matter. Flagellates in freshwater ponds are certainly subject to aggregation. Larger forms such as the plankton copepods are certainly subject to swarming, as Hardy (1936) has shown, and as may be seen in the graphs of distribution published in the various numbers of the Hull Bulletins of Marine Ecology. Barnes & Marshall (1951) have shown that such aggregations of plankton copepods and nauplii may occur in the sea over a scale of metres or tens of metres. There may well be patchiness on a much smaller scale than hitherto described. Bainbridge (1953) has shown that copepods will move into patches of food organisms. If this aggregation of both the flagellates and the plankton copepods occurs on a fairly small scale, normal filter feeding might well account for the observed survival and growth. The observations on swarming quoted by Bainbridge are of interest, for if a patch of water supports a very dense shoal of plankton for a while it will become enriched in nitrogenous substances and therefore cause in due course a localized bloom of phytoplankton organisms if there is enough light, or of colourless flagellates and bacteria if there is not.

These two possible methods have in common the principle that the copepod needs to conduct active search for either its prey or for a patch of filterable material. Which of these methods occurs it is not, in the present state of knowledge, possible to say. In either case, the presence of large numbers of nauplii and of young copepodite stages in the winter months may be expected to be of even greater importance to the economy of the plankton population in polar waters than in temperate waters, because the phytoplankton is much scarcer in winter. The smaller sizes of zooplankton organisms would be more easily caught by a predator when alive, or when killed by parasites or other agencies would sink to the bottom less rapidly and would therefore be available as food in the surface layers for a longer time.

The proportion of smaller to larger forms in Scoresby Sound was at least as great as in temperate waters. The abundance of all species drawn to the same scale and expressed in numbers per cubic metre is shown in Fig. 15. All species numerous enough to show on the scale are included, with the exception of the harpacticids, *Microsetella* and *Ectinosoma*. This diagram may be compared with that given by Marshall (1949) for the copepods of Loch Striven, and by Digby (1950) for those of the English Channel. It demonstrates very clearly the numerical superiority of *Oithona* throughout the year, which is rather more marked than in Loch Striven or the English Channel, and it also demonstrates the presence of large numbers of nauplii of one species or another at all times of the year even though the period of phytoplankton production is so short.

(*b*) *The change in size*

The stages of *Calanus*, *Pseudocalanus* and *Microcalanus* in particular exhibit an increase in size in both summer and winter. The summer increase in size, as Ussing pointed out and as is demonstrated here, occurs over the period of phytoplankton production and, since the temperature varies little throughout the year, the size increase may be attributed to the good feeding conditions at the time.

Ussing described a considerable lag in the attainment of maximum size of successive stages in *Calanus* and *Pseudocalanus*, and therefore suggested the size to which a copepod moulted was dependent on two factors, the size before moulting and the

nutrition at the time of the moult. In this material the delay between the attainment of maximum size in successive stages is shown to be at the most a week per stage, while

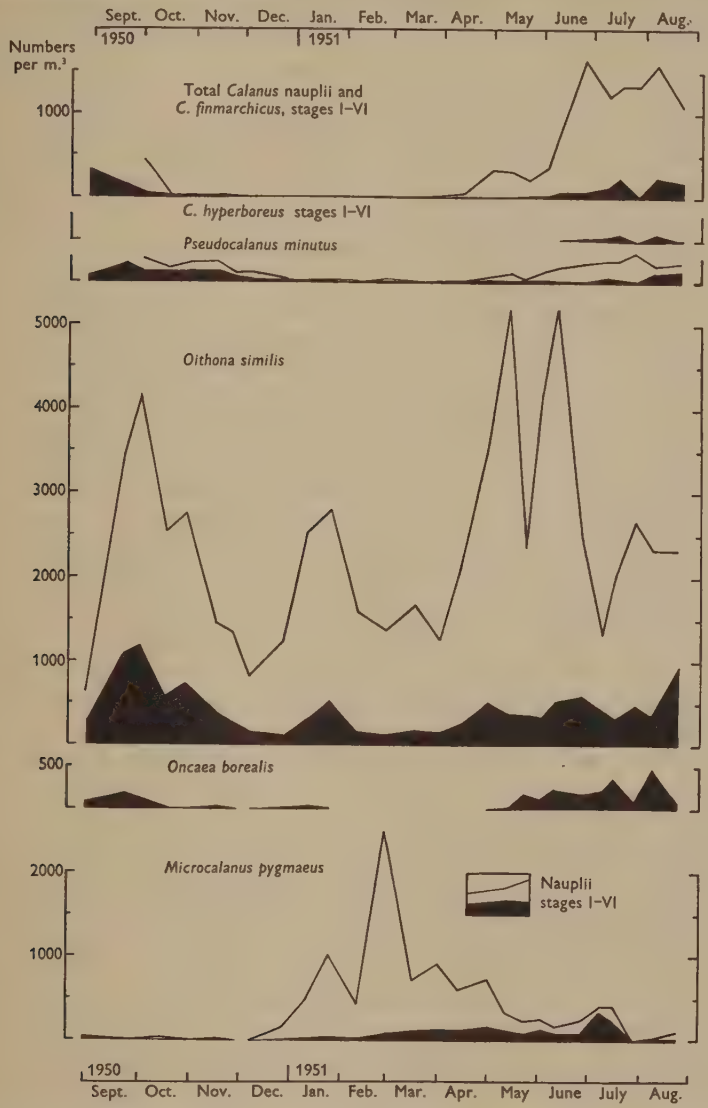

Fig. 15. Abundance of the more common copepods, as nauplii and stages I–VI, all drawn to the same scale. Numbers less than 10/m.³ omitted. Harpacticids, although having maxima of about 20/m.³, are omitted as not assessed quantitatively.

the time taken for a copepod to develop over one stage is about a month, so it is concluded that the size before moulting has comparatively little effect on the size following the moult, most of the size-change being a function of nutrition. Ussing described

how the increase of size with a phytoplankton outburst can give rise to such diverse size effects as to result in the bimodal size-distribution of late stages of *Calanus* and the unimodal size-groups of *Pseudocalanus* and *Metridia*, according to whether a group of individuals consists of members which were formed under differing or under uniform conditions of nutrition. The conclusions reached in this paper, which are discussed in the sections dealing with the life-histories of the individual copepods, support this in principle. It is however considered that this present material suggests that the situation with regard to *Calanus* is rather more complicated, in that although the bimodal nature of the size-groups has arisen in this manner, there is an admixture of the stock from two year groups, some individuals being of the order of one year old and some two years old at any given time. Furthermore, in *Metridia* the long period in which the individuals were present in the surface water through the year makes it seem probable that some moulting occurred during the period of phytoplankton production, but the size-groups of stage V and of the adults are very compact. In this case also there may be more in the limited size-distribution than just the period of moulting. It might be suggested that a small variation in size would arise if a species lived at depth in summer, for with increasing depth the conditions of nutrition become more even. However, *Microcalanus*, which like *Metridia* passes the summer below the 50 m. level, shows a very considerable spread in size. One may suggest there may be a variation in the degree to which the various copepods have the ability to feed on a high density of phytoplankton and assimilate at a high rate in periods of abundant food. *Metridia*, which can develop in winter and lives deep in summer, may be adapted to a low rate of feeding.

The mid-winter rise is a remarkable feature of this material. Ussing found *Microcalanus*, *Metridia* and *Pareuchaeta* appeared in mid-winter and sank in summer, and this is confirmed in this material, but here some large specimens of *Calanus* and *Pseudocalanus* are shown to behave in the same way. The increase in size appears to be to a certain extent a function of the size of the copepod. Of the species for which we have the most abundant size data it was most well marked in *Calanus*, less well marked in *Pseudocalanus* and only suggested in *Oithona*. Of the other species for which we have less abundant data, it is shown by *Calanus hyperboreus* possibly better than by the smaller *C. finmarchicus* and also by *Oncaea*. *Microcalanus* is the exception, for, bearing in mind that from the way in which the size-group diagram (Fig. 13) has been constructed, the large group appears relatively more abundant. *Microcalanus*, in spite of its small size, shows this winter rise to as marked an extent as does *Calanus*. In *Calanus*, *Pseudocalanus* and *Microcalanus*, the winter size-increase is most marked in the later and least marked or absent in the earlier stages. In *Oithona* there is a suggestion of the same thing, in that whereas the sizes of stages III and IV show a decline through winter, those of stages V and VI remain fairly level, as if the decline which might be expected, were there no winter rise, was offset by a small amount of size-increase due to the upward movement of large individuals.

This effect has been considered hitherto to be a real rise of large specimens in mid-winter. But it is necessary to consider another alternative, that is, that the effect may be caused by the large copepods escaping the nets during the light period when it can be seen, and not during the winter. Attention was drawn in the introduction to the loss

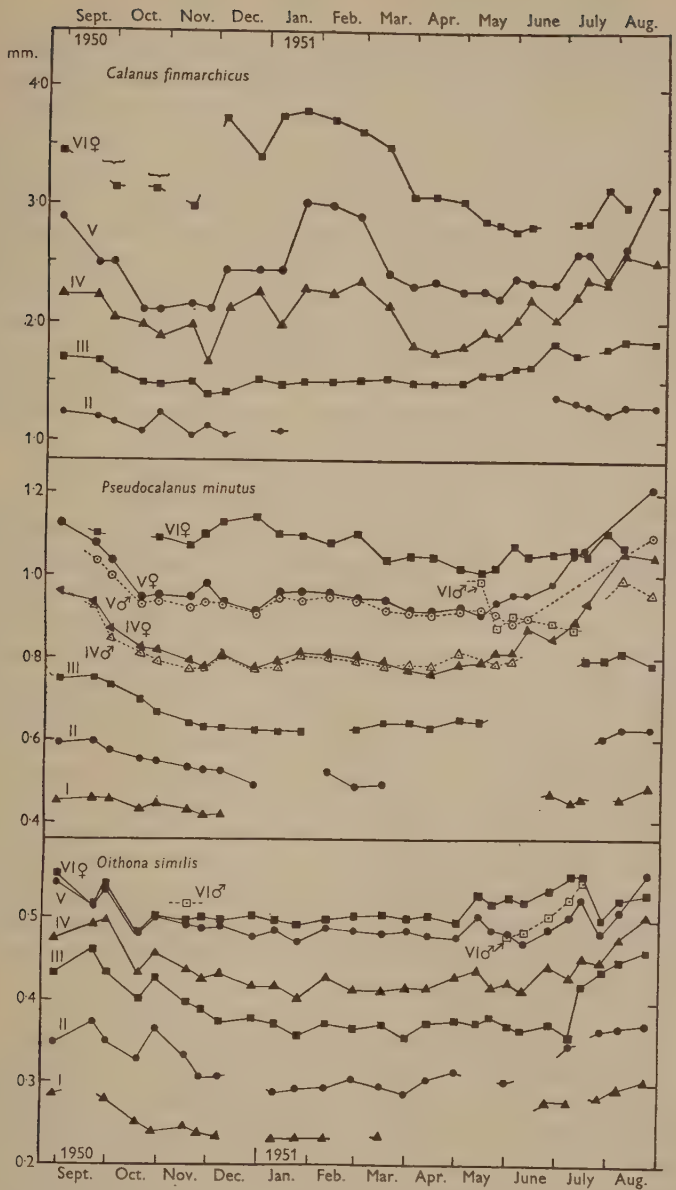

Fig. 16. *Calanus finmarchicus*, *Pseudocalanus minutus* and *Oithona similis*, median size-curves, showing the differences in the extent of the mid-winter increase in size, most marked in later stages of *Calanus*, less well marked in *Pseudocalanus* and almost or completely absent in *Oithona*; and the very slight lag between the time of attainment of the maximum median size in successive stages in summer.

of large *Calanus* from the path of the net. However, *Microcalanus* shows the size-increase just as does *Calanus*, and it seems unlikely that such a small form would be able to escape the 50 cm. net. Furthermore, were it to be an effect of selective escape, it would be expected to show much more markedly in the smaller net with the 12·5 cm. aperture than in the larger 50 cm. net. *Calanus* did not appear in sufficient numbers in the small net for a comparison to be made, but in *Pseudocalanus* it did not appear to be the case. Moreover, large specimens are taken, of course, in mid-summer when larger *Calanus* are known to occupy deeper water layers (Jespersen 1934, 1939*a*). It is therefore reasonable to suppose that although in *Calanus* it is quite possible that the winter size-increase may be enhanced by selective escape of large individuals during the period when it was light enough for them to see the nets, the increase in median size, as has been contended so far, is due mainly to the upward movement of large individuals from below the 50 m. level, comparable in some way to that which is the main movement in the species which appear in the surface in winter, and the specimens which take part most actively are the largest because of their superior mobility.

(*c*) *The vertical movements*

It remains to consider the mechanisms of these upward movements in mid-winter. Ussing pointed out the two groups of copepods as representing two different reaction types, the *Calanus* type, which rises to the surface in summer and sinks in winter, and the *Metridia* type, which sinks in summer and rises to the surface in winter. He suggested that the essential difference between the two types depended on whether they could maintain their level in the water, or rise, in darkness or not. The winter rise in *Calanus* at Scoresby Sound does not support this idea, because the differences between the *Calanus* and *Metridia* types of reaction would now seem to be only that *Metridia* lives at a deeper level in summer than does *Calanus*, as is known from the material described by Jespersen (1939*a*). Both species exhibit diurnal migrations and both rise to the surface in winter.

It may perhaps not be out of place to suggest some pattern of reactions that might explain the rise in both summer and winter in *Calanus*. Sømme (1934) considered that a decrease of light over a long period probably caused a decrease of activity in *Calanus*, the copepod becoming lethargic and sinking, and the rising in the spring was attributed to increased activity and upward movement in light. Conversely, many investigations (see Schallek 1942) have shown an increase of light to cause a movement downwards and a decrease to cause movement upwards, although the precise way in which it works seems to vary from one species to another. Schallek (1942, 1943) showed that *Acartia tonsa* would either rise towards a light or sink according to whether the light was diffuse or highly directional, but concluded that under natural conditions the light was always diffuse enough to cause sinking rather than rising. If these antagonistic effects operate in the sea, that is, the effect of a decrease in light causes a sinking over a long period of time and the short-term changes in light cause diurnal vertical migrations, the pattern of events including the mid-winter rise may be explained.

In summer, specimens may be maintained in the surface layers by the high light intensity causing a general high level of activity. Diurnal changes in the light, where

obvious, cause diurnal migrations. Bogorov (1946*b*) has shown these diurnal migrations in arctic waters to be more marked in autumn when there are differences in light similar to the day and night of temperate latitudes and to be less marked or absent in mid-summer when the light conditions are much more uniform. In autumn the seasonal reduction in light causes an overall reduction in activity resulting in sinking, and in early summer the increased level of light intensity causes an enhanced level of activity which results in the stock rising to the surface once more. The mid-winter rise in *Calanus* cannot be explained if we assume the sinking in winter to be an entirely passive affair. But the specimens caught in winter were very active and it seems not unlikely that some small amount of diurnal migration may go on throughout the year whatever the average position of the stock so long as they can appreciate any diurnal differences in the light intensity. Now in winter the 'light' period of the 24 hr. is restricted to 3 hr. or so of twilight at Scoresby Sound, the rest of the time being dark apart from the much fainter illumination afforded by moonlight and by the Northern Lights. If these twilight to night-time changes in light intensity are sufficient to stimulate diurnal movements, there might well be a long period of upward movement each 'night', following and stimulated by the 2 hr. or so of failing light, and a short downward movement each 'day' following and stimulated by the 2 hr. or so of increasing light. If this were the case, the net result could well be a rise in the stock in mid-winter, sufficient to override the effect of sinking caused by the decreased level of activity, whereas on either side of mid-winter with the longer 'day' and shorter 'night' the diurnal movements might well be more evenly balanced, resulting in a lower level of the stock at these times than in mid-winter. This suggested explanation depends on *Calanus* below 50 m. of water and 2 or 3 ft. of snow and ice being able to appreciate the difference between night and the twilight of the arctic day in mid-winter. In view of the apparent light sensitivity of some of the species of plankton animals which habitually migrate to and from very deep water, this seems not altogether impossible.

One test of the above suggestion would be given by the changes through winter in the size-distribution of these species farther north where the winter darkness is not relieved by twilight at midday. If *Calanus* still showed a rise in size about mid-winter under these conditions it would mean the reactions suggested above are incorrect, whereas if the size showed an additional decrease in the darkest period when night and day were not at all distinguishable it would support these suggestions.

ACKNOWLEDGEMENTS

I am indebted to the Royal Society Trustees of the Browne Fund and to the many people mentioned in a previous paper (Digby 1953) for their manifold assistance, and to Dr J. P. Harding for the identification of *Bradyetes brevis*. I am most grateful to Dr S. M. Marshall and Dr A. P. Orr for reading the manuscript and for their most helpful suggestions. I am particularly indebted to my wife for her help in both field and laboratory.

SUMMARY

1. An account is given of the abundance and size-changes of the common marine planktonic copepods of Scoresby Sound, East Greenland. It is based on measuring net hauls taken in the upper 50 m. of water throughout the year from August 1950 to August 1951.

2. The species concerned were *Calanus finmarchicus*, *C. hyperboreus*, *Pseudocalanus minutus*, *Oithona similis*, *Oncaea borealis*, *Microcalanus pygmaeus*, *Metridia longa* and species of *Pareuchaeta*. Species other than these were taken only in small numbers.

3. The account of the seasonal abundance of stages of *Calanus*, *Pesudocalanus* and *Metridia* confirms previous work on this coast. The seasonal abundance of the stages of *Oithona*, *Oncaea* and *Microcalanus* are described in detail for polar water for the first time.

4. In *Calanus finmarchicus* it is suggested that some of the specimens hatched each summer may possibly have attained maturity as small individuals that same autumn below the 50 m. level. Most of the remainder reached maturity in the following summer, first of all as small specimens, then as large according to the phytoplankton, and a certain number survived through yet another year, as large late stages. It is held that although food conditions were responsible for the changes in size, the life-history was such that the large and small groups of the late stages often represented different year-groups.

5. *Calanus hyperboreus*, breeding earlier than *C. finmarchicus*, exhibited unimodal size-groups in the late stages and probably came to maturity in one year.

6. In *Pseudocalanus* most of the individuals passed through one generation in a year, those hatching in summer reaching maturity that autumn or winter as a numerically large group of adults of small size. Some moulted to the mature state the following summer and appeared as a minority of individuals of large size, while some of these apparently survived a second winter.

7. In *Oithona* most of the individuals passed through one generation a year, but some passed through two.

8. *Microcalanus* passed through one generation at the surface, most of the young stages developing early in the year before the phytoplankton. It may have had a second generation below the 50 m. level over the period of phytoplankton production. It showed a wide size variation like that of *Pseudocalanus*.

9. *Metridia* and *Pareuchaeta* appeared to pass through one generation in the year, breeding in the depths over summer.

10. The species which developed through summer appeared able to pass through their life-cycle in about 20 weeks at that temperature, were the phytoplankton conditions suitable for such a period; but those which developed in winter, *Microcalanus* and *Metridia*, appeared to take longer.

11. Although little, if any, development of *Calanus* and *Pseudocalanus* went on outside the period of phytoplankton abundance, *Microcalanus* at any rate developed through several stages in winter, and this can only mean that some form of predacious feeding went on. *Microcalanus* has not the strongly raptorial mouthparts usually associated with the carnivorous habit. The other apparently filter-feeding copepods

may also obtain enough food in winter by predation to enable them to survive without reducing their metabolic rate. Nauplii and small stages of *Oithona* which might serve as food for larger copepods were present in considerable numbers all the year.

12. There were two periods of size-increase. The summer increase, evident in all stages of all species, was due to growth under good phytoplankton conditions; there was a lag of about a week between the time of attainment of maximum size of one copepodite stage and that of the next more advanced stage. The development time from stage to stage was about a month, and therefore the size attained by a copepod on moulting from one stage to the next was due almost entirely to the state of nutrition at the time of the moult, and the effect of the size of the preceding stage was slight.

13. The winter size-increase, hitherto undescribed, was shown by the later stages of *Calanus* and *Pseudocalanus* and occurred simultaneously in all the stages concerned. It is attributed to upward movement of large individuals formed in summer which had sunk to lower levels than the smaller individuals in the autumn and again in the spring. This mid-winter increase in size indicates that some individuals of *Calanus finmarchicus* and *Pseudocalanus* survive for 2 years.

REFERENCES

Adler, G. & Jespersen, P. (1920). Variations saisonnières chez quelques copépodes planktoniques marins. *Medd. Komm. Havundersøg., Kbh.* (Serie plankton), **2**, 1–46.

Bainbridge, R. (1953). Studies on the interrelationships of zooplankton and phytoplankton. *J. Mar. Biol. Ass. U.K.* **32**, 385–447.

Barnes, H. & Marshall, S. M. (1951). On the variability of replicate plankton samples and some applications of 'contagious' series to the statistical distribution of catches over restricted periods. *J. Mar. Biol. Ass. U.K.* **30**, 233–63.

Bogorov, B. G. (1946*a*). Zooplankton collected by the expedition in the icebreaker 'G. Sedov' 1937–39; in Buynitskiy, V.Kh., ed. *Transactions of the drifting expedition of the Chief Administration of the Northern Sea Route in the icebreaker 'G. Sedov'* 1937–40, **3**, 336–70. Moscow, Leningrad.

Bogorov, B. G. (1946*b*). Peculiarities of diurnal vertical migrations of zooplankton in polar seas. *J. Mar. Res.* **6**, 25–32.

Deevey, G. B. (1952*a*). A survey of the zooplankton of Block Island Sound, 1943–1946. *Bull. Bingham Oceanogr. Coll.* **13**, 65–119.

Deevey, G. B. (1952*b*). Quantity and composition of the zooplankton of Block Island Sound, 1949. *Bull. Bingham Oceanogr. Coll.* **13**, 120–64.

Damas, D. & Koefoed, E. (1909). Le Plankton de la Mer du Grönland. In: *Duc D'Orleans Croisière Océanographique accomplié à bord de la Belgica dans la Mer du Grönland*, 1905: pp. 347–453.

Digby, P. S. B. (1950). The biology of the small planktonic copepods of Plymouth. *J. Mar. Biol. Ass. U.K.* **29**, 393–438.

Digby, P. S. B. (1953). Plankton production in Scoresby Sound, East Greenland. *J. Anim. Ecol.* **22**, 289–322.

Farran, G. P. (1936*a*). The arctic plankton collected by the 'Nautilus' Expedition, 1931. Part II, Report on the Copepoda. *J. Linn. Soc. (Zool.)*, **39**, 404–10.

Farran, G. P. (1936*b*). *Bradyetes brevis*, a new species of copepod from East Greenland. *Ann. Mag. Nat. Hist.* (10), **18**, 238–41.

Fish, C. J. (1936*a*). The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, **70**, 118–41.

Fish, C. J. (1936*b*). The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, **70**, 193–216.

Fish, C. J. (1936*c*). The biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, **71**, 168–87.

Fuller, J. L. (1937). Feeding rate of *Calanus finmarchicus* in relation to environmental conditions. *Biol. Bull., Woods Hole*, **72**, 233–46.

Fuller, J. L. & Clarke, G. L. (1936). Further experiments on the feeding of *Calanus finmarchicus*. *Biol. Bull., Woods Hole*, **70**, 308–20.

Gauld, D. T. (1951). The grazing rate of planktonic copepods. *J. Mar. Biol. Ass. U.K.* **29**, 695–706.

Gran. H. H. (1902). Das Plankton des norwegischen Nordmeeres von biologischen und hydrographischen Gesichtspunkten behandelt. *Rep. Norweg. Fish. Invest.* **2**, part 2, no 5, 1–222.

Hardy, A. C. (1936). Observations on the uneven distribution of the oceanic plankton. *Discovery Rep.* **11**, 511–38.

Harvey, H. W. (1937). Note on selective feeding by *Calanus*. *J. Mar. Biol. Ass. U.K.* **22**, 97–100.

Harvey, H. W. (1950). On the production of living matter in the sea off Plymouth. *J. Mar. Biol. Ass. U.K.* **29**, 97–137.

Harvey, H. W., Cooper, L. H. N., Lebour, M. V. & Russell, F. S. (1935). Plankton production and its control. *J. Mar. Biol. Ass. U.K.* **20**, 407–42.

Jespersen, P. (1934). The Godthaab Expedition 1928: Copepoda. *Medd. Grønland.* **79** (10), 1–166.

Jespersen, P. (1939*a*). Investigations on the Copepod Fauna in East Greenland Waters. *Medd. Grønland.* **119** (9), 1–106.

Jespersen, P. (1939*b*). The Zoology of East Greenland, Copepods. *Medd. Grønland.* **121** (3), 1–66.

Lebour, M. V. (1916). Stages in the life history of *Calanus finmarchicus* (Gunnerus), experimentally reared by Mr L. R. Crawshay in the Plymouth laboratory. *J. Mar. Biol. Ass. U.K.* (N.S.), **11**, 1–17.

Lebour, M. V. (1922). The food of plankton organisms. *J. Mar. Biol. Ass. U.K.* **12**, 644–77.

Lowndes, A. G. (1935). The swimming and feeding of certain Calanoid copepods. *Proc. Zool. Soc. Lond.* pp. 687–715.

Lucas, C. E. (1936). On certain inter-relations between phytoplankton and zooplankton under experimental conditions. *J. Cons. int. Explor. Mer.* **II** (3), 343–62.

Mackintosh, N. A. (1937). The seasonal circulation of the Antarctic macroplankton. '*Discovery*' *Rep.* **16**, 365–412.

Marshall, S. [M.] (1923). The food of *Calanus finmarchicus* during 1923. *J. Mar. Biol. Ass. U.K.* (N.S.) **13**, 473–9.

Marshall, S. M. (1933). On the biology of *Calanus finmarchicus*. II. Seasonal variations in the size of *Calanus finmarchicus* in the Clyde Sea-Area. *J. Mar. Biol. Ass. U.K.* **19**, 111–38.

Marshall, S. M. (1949). On the biology of the small copepods in Loch Striven. *J. Mar. Biol. Ass. U.K.* **28**, 45–122.

Marshall, S. M., Nicholls, A. G., & Orr, A. P. (1934). On the biology of *Calanus finmarchicus*. V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933, and their relation to the phytoplankton. *J. Mar. Biol. Ass. U.K.* **19**, 793–827.

Marshall, S. M. & Orr, A. P. (1952). On the biology of *Calanus finmarchicus*. VII. Factors affecting egg production. *J. Mar. Biol. Ass. U.K.* **30**, 527–48.

Moore, H. B. (1931). The muds of the Clyde Sea Area. III. Chemical and physical conditions; rate and nature of sedimentation; and fauna. *J. Mar. Biol. Ass. U.K.* (N.S.), **17**, 325–58.

Nicholls, A. G. (1933). On the biology of *Calanus finmarchicus*. I. Reproduction and seasonal distribution in the Clyde Sea-Area during 1932. *J. Mar. Biol. Ass. U.K.* **19**, 83–109.

Oberg, M. (1906). Die Metamorphose der Plankton-Copepoden der Kieler Bucht. *Wiss. Meeresuntersuch.* (Abt. Kiel), **9**, 37–175.

Ottestad, P. (1932). On the biology of some southern Copepoda. *Hvalrâd. Skr.* no. 5, 1–61.

Rees, C. B. (1949). Continuous plankton records: the distribution of *Calanus finmarchicus* (Gunn.) and its two forms in the North Sea, 1938–39. *Hull. Bull. Mar. Ecol.* **2** (14), 215–75.

Russell, F. S. (1931). The Zooplankton. I. Gear, methods and station lists. *Great Barrier Reef Expedition*, 1928–9. *Sci. Rept.* **2** (2), 2–36.

Sars, G. O. (1900). Crustacea. *The Norwegian North Polar Expedition*, 1893–96. *Sci. Res.* **5**.

Sars, G. O. (1903). *An account of the Crustacea of Norway*, **4**. *Copepoda Calanoidea*. Bergen.

Schallek, W. (1942). The vertical migration of the copepod *Acartia tonsa* under controlled illumination. *Biol. Bull., Woods Hole*, **82**, 112–26.

Schallek, W. (1943). The reaction of certain crustacea to direct and to diffuse light. *Biol. Bull., Woods Hole*, **84**, 98–105.

Shirshov, P. P. (1938). Oceanological observations. *C.R. Acad. Sci. U.R.S.S.* **19** (8), 569–80.

Sømme, J. D. (1934). Animal plankton of the Norwegian coast waters and the open sea. I. Production of *Calanus finmarchicus* (Gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten area. *Rep. Norweg. Fish. Invest.* **4** (9), 1–163.

Størmer, L. (1929). Copepods from the 'Michael Sars' Expedition, 1924. *Rapp. Cons. Explor. Mer*, **56** (7), 1–57.

Ussing, H. H. (1938). The biology of some important plankton animals in the fiords of East Greenland. *Medd. Grønland.* **100** (7), 1–108.

Vanhöffen, E. (1897). *Die Fauna und Flora Grönlands. Drygalski: Grönland-Expedition der Gesellschaft für Erdkunde, Berlin*, 1891–93.

Wirborg, K. F. (1944). The production of zooplankton in a land-locked fjord, the Nordåsvatn near Bergen, in 1941–42 with special reference to the copepods. *Rep. Norweg. Fish. Invest.* **7** (7), 1–83.

With, C. (1915). Copepoda I. Calanoida Amphaskandria. *The Danish Ingolf Expedition*, **3** (4). Copenhagen.

APPENDIX

Table 1. Calanus finmarchicus *and* C. hyperboreus: *abundance in numbers per cubic metre.*

(Numbers of *C. finmarchicus* nauplii and occasionally stage I from fine net, later stages from coarse net; numbers of *C. hyperboreus* from coarse net. + indicates numbers below 0·5/m.³.)

	C. finmarchicus and *C. hyperboreus*	*C. finmarchicus*						*C. hyperboreus*					
Date	Nauplii	I	II	III	IV	V	VI♀	VI♂	II	III	IV	V	VI♀	VI♂
1950														
29 Aug.	.	33	116	129	20	19	1	.	.	2	1	1	+	.
21 Sept.	.	36	30	46	30	3	+	.	1	1	3	.	.	.
30 Sept.	378	14	10	14	12	12	+	.	.	.	.	.	.	.
18 Oct.	.	2	7	9	4	1	+	.	.	.	.	.	.	.
28 Oct.	.	1	5	19	9	4	+	.	.	.	.	.	.	.
16 Nov.	.	+	2	13	4	1	+	.	+	.	.	.	.	.
25 Nov.	.	+	1	5	1	+	+	+	+	.	.	.	.	.
6 Dec.	.	.	2	10	2	1	+	+	.	.	.	.	+	.
26 Dec.	.	.	1	10	2	1	+	+	.	.	+	+	+	.
1951														
9 Jan.	.	.	+	4	1	1	1	+	.	+	.	+	+	.
23 Jan.	10	.	+	3	1	+	+	+	.	.	.	.	+	.
9 Feb.	5	.	+	3	1	1	1	+	.	+	+	.	+	.
26 Feb.	.	.	+	+	+	+	+	.	.	.	.	.	.	.
15 Mar.	6	.	+	1	+	+	+	+	.	.	.	+	.	.
30 Mar.	24	.	+	+	+	+	+	.	.	.	+	+	.	.
12 Apr.	52	.	.	1	+	1	+	+	.	+	+	+	.	.
29 Apr.	319	.	+	5	1	+	1	+	.	.	.	.	.	.
12 May	294	.	+	8	2	2	1	.	+	.	.	.	.	.
21 May	184	2	+	10	9	3	1	+	+	+	+	.	.	.
31 May	318	3	+	10	5	8	3	+	+	+	+	+	.	.
9 June	690	31	7	6	22	11	3	.	4	.	1	1	.	.
24 June	1569	64	5	+	1	1	.	.	31	1	+	.	.	.
7 July	1079	71	10	3	21	22	4	.	33	13	1	2	+	.
14 July	1106	164	3	5	14	40	6	.	22	40	5	4	+	.
26 July	1288	18	12	4	1	2	1	.	.	.	+	.	.	.
6 Aug.	1316	153	43	15	6	20	7	.	35	23	4	2	+	.
23 Aug.	905	90	52	37	10	3	+	.	2	13	5	+	.	.

Table 2. Pseudocalanus minutus: *abundance in numbers per cubic metre*

(Nauplii to stage II in summer when nets clogged and to stage IV in winter from fine net, remaining stages from coarse net. + indicates numbers below 0·5/m.³.)

Date	Nauplii	I	II	III	IV	V	VI♀	VI♂
1950								
29 Aug.	(not	14	18	19	18	10	1	.
21 Sept.	assessed)	46	60	38	31	52	2	.
30 Sept.	139	22	23	22	27	40	2	.
18 Oct.	43	10	11	13	16	83	1	.
28 Oct.	75	10	16	12	15	93	1	.
16 Nov.	110	15	20	25	25	50	2	+
25 Nov.	59	6	8	10	8	19	1	.
6 Dec.	92	3	4	7	3	19	1	+
26 Dec.	5	+	3	6	4	11	1	.
1951								
9 Jan.	10	5	1	5	4	8	1	.
23 Jan.	10	1	2	4	3	6	1	+
9 Feb.	10	1	5	1	2	7	1	+
26 Feb.	21	2	3	7	7	10	2	.
15 Mar.	9	1	2	2	4	7	2	+
30 Mar.	2	.	+	1	2	7	3	+
12 Apr.	5	+	1	2	3	8	5	+
29 Apr.	30	+	+	3	3	13	19	+
12 May	90	.	.	1	2	4	10	+
21 May	20	.	.	+	3	9	18	1
31 May	106	.	+	3	5	14	15	3
9 June	180	1	+	1	5	6	3	1
24 June	209	4	1	1	2	2	8	2
7 July	190	42	3	2	2	8	15	1
14 July	230	21	5	2	2	5	12	1
26 July	334	4	8	7	1	+	1	.
6 Aug.	100	34	19	23	21	4	12	.
23 Aug.	105	39	14	19	42	9	2	.

Table 3. Oithona similis: *abundance in numbers per cubic metre from catches of fine net*

(+ indicates numbers below 0·5/m.³.)

Date	Eggs	Nauplii	I	II	III	IV	V	VI♀	VI♂
1950									
29 Aug.	875	358	44	48	35	28	30	94	4
21 Sept.	2024	2360	211	361	234	92	109	87	1
30 Sept.	979	3003	86	341	394	183	81	88	1
18 Oct.	229	1949	116	132	182	99	38	18	.
28 Oct.	253	2031	84	253	139	174	56	22	1
16 Nov.	87	2030	48	48	89	104	56	47	4
25 Nov.	20	1050	34	52	68	83	20	21	1
6 Dec.	1	675	12	41	44	31	14	12	1
26 Dec.	.	1108	10	16	19	38	15	19	1
1951									
9 Jan.	.	2195	26	65	57	100	40	40	1
23 Jan.	.	2266	50	131	156	128	26	31	.
9 Feb.	4	1420	18	44	52	37	12	15	+
26 Feb.	.	1235	7	26	38	36	8	10	.
15 Mar.	16	1478	18	27	62	50	20	15	+
30 Mar.	.	1105	14	34	42	36	16	10	.
12 Apr.	45	1845	8	57	70	66	29	29	+
29 Apr.	2	3017	25	75	137	127	84	65	.
12 May	25	4802	.	35	71	150	67	70	1
21 May	50	1980	.	20	44	129	140	53	1
31 May	130	3820	6	34	66	101	84	49	2
9 June	100	4660	34	8	77	121	168	102	5
24 June	560	1911	128	33	65	50	172	110	24
7 July	539	905	81	12	19	48	95	147	18
14 July	1802	1700	43	43	64	5	82	74	25
26 July	863	2184	252	84	23	13	41	55	4
6 Aug.	2263	1981	135	108	73	18	3	9	7
23 Aug.	1007	1446	288	243	151	46	47	126	2

Table 4. Oncaea borealis: *abundance in numbers per cubic metre, from catches of fine net*

(+ indicates specimens present in coarse net only or in fine net below 0·5/m.³.)

Date	I	II	III	IV	V	VI♀	VI♂
1950							
29 Aug.	1	1	25	28	25	3	14
21 Sept.	.	.	41	43	6	2	82
30 Sept.	.	1	1	10	84	1	30
18 Oct.	.	.	.	.	5	1	+
28 Oct.	.	.	.	5	1	1	2
16 Nov.	1	4	4	+	5	4	22
25 Nov.	+	+	.	.	.	1	1
6 Dec.	1	1	.	.	.	.	1
26 Dec.	.	.	.	.	1	5	10
1951							
9 Jan.	6	10	1	.	.	2	7
23 Jan.	.	.	.	.	.	1	5
9 Feb.	1	2	.	.	+	1	1
26 Feb.	2	2	.	.	.	.	.
15 Mar.	.	1	.	.	.	+	.
30 Mar.	.	.	.	.	.	+	.
12 Apr.	.	4	.	.	.	+	.
29 Apr.	.	.	.	.	.	1	.
12 May	.	15	.	.	.	1	5
21 May	.	67	94	.	.	15	7
31 May	.	72	24	6	2	+	14
9 June	.	133	81	7	.	2	14
24 June	.	100	60	11	10	3	11
7 July	7	74	95	41	8	1	13
14 July	.	140	140	80	1	4	.
26 July	.	28	42	21	10	.	.
6 Aug.	.	120	220	62	2	8	60
23 Aug.	.	7	.	34	28	.	20

Table 5. Microcalanus pygmaeus: *abundance in numbers per cubic metre, from catches of fine net*

(+ indicates specimens present in coarse net only or in fine net below 0·5/m.³.)

Date	Nauplii	I	II	III	IV	V	VI♀	VI♂
1950								
29 Aug.	22	5	11	8	8	4	10	1
21 Sept.	40	.	.	2	4	.	1	.
30 Sept.	10	.	.	.	.	.	.	.
18 Oct.	37	1	+	.	+	.	.	.
28 Oct.	.	.	.	+	+	.	.	.
16 Nov.	21	4	4	4	4	2	6	+
25 Nov.	.	+	.	+	1	+	1	+
6 Dec.	2	1	.	1	+	+	1	+
26 Dec.	145	5	+	+	2	1	4	.
1951								
9 Jan.	439	19	9	4	4	2	7	+
23 Jan.	983	5	15	6	2	2	3	.
9 Feb.	416	7	5	5	4	1	5	+
26 Feb.	2407	36	22	13	5	2	6	+
15 Mar.	621	45	23	22	9	1	5	.
30 Mar.	785	66	44	16	8	.	3	.
12 Apr.	490	48	30	26	11	3	6	.
29 Apr.	565	45	50	36	18	18	3	+
12 May	240	25	45	10	21	4	3	.
21 May	160	13	20	28	19	8	1	.
31 May	114	26	38	24	15	33	3	.
9 June	80	20	21	15	10	15	1	.
24 June	140	48	19	15	10	1	+	+
7 July	80	70	152	101	13	5	1	1
14 July	182	40	83	79	27	5	1	+
26 July	.	.	.	.	.	.	.	.
6 Aug.	.	.	6	8	6	.	.	.
23 Aug.	79	.	3	22	7	.	1	.

Table 6. Metridia longa: *abundance in numbers per cubic metre, from catches of fine and coarse nets combined*

(Stage I from fine net, remainder from coarse net. + indicates numbers below 0·5/m.³.)

Date	I	II	III	IV	V	VI♀	VI♂
1950							
29 Aug.	.	.	.	.	+	1	.
21 Sept.	.	.	1	1	2	.	.
30 Sept.	.	.	.	+	1	2	.
18 Oct.	1	+	.	.	+	.	.
28 Oct.	.	.	.	.	.	+	.
16 Nov.	1	1	+	+	+	.	.
25 Nov.	.	+	+	+	+	.	+
6 Dec.	.	+	+	+	1	+	+
26 Dec.	.	1	1	1	+	+	+
1951							
9 Jan.	+	+	1	1	+	+	.
23 Jan.	.	+	+	+	+	+	+
9 Feb.	.	+	1	1	1	+	+
26 Feb.	.	+	1	2	1	+	.
15 Mar.	.	+	+	+	+	.	.
30 Mar.	.	.	+	+	+	+	.
12 Apr.	.	.	.	+	+	.	.
29 Apr.	+	.	+	+	.	.	.
12 May	+	.	.	.	.	.	.
21 May	.	.	.	+	+	.	.
31 May	.	.	.	+	.	.	.
9 June	+	.	.	.	.	.	.
24 June	+	.	.	.	.	.	.
7 July	3	+	.	.	+	+	.
14 July	1	+	.	+	.	.	.
26 July	.	.	.	.	.	.	.
6 Aug.	.	.	.	.	.	+	.
23 Aug.	.	.	+	.	.	.	.

Table 7. Pareuchaeta *spp.*: *abundance in numbers per cubic metre, from catches of coarse net*

(+ indicates specimens present below 0·5/m.³.)

Date	I	II	III	IV	V	VI♀	VI♂
1950							
29 Aug.	.	+	.	.	.	.	.
21 Sept.	.	+	+	+	+	.	.
30 Sept.	.	.	.	.	.	.	.
18 Oct.	.	+	.	.	.	.	.
28 Oct.	.	.	+	.	.	.	.
16 Nov.	.	+	+	.	.	.	.
25 Nov.	.	.	+	.	.	.	.
6 Dec.	.	+	+	+	+	.	.
26 Dec.	.	+	+	+	+	.	.
1951							
9 Jan.	+	+	+	+	+	.	.
23 Jan.	.	.	+	+	.	.	.
9 Feb.	.	.	+	+	+	.	.
26 Feb.	.	.	.	.	.	.	.
15 Mar.	+	+	+	+	.	.	.
30 Mar.	+	+	+	.	.	.	.
12 Apr.	.	+	+	.	.	.	.
29 Apr.	.	+	.	.	.	.	.
12 May	+	+	+	.	.	.	.
21 May	.	+	.	.	.	.	.
31 May	.	.	.	.	.	.	.
9 June	.	.	.	.	.	.	.
24 June	.	.	.	.	.	.	.
7 July	.	.	.	.	.	.	.
14 July	.	.	.	.	.	.	.
26 July	.	.	.	.	.	.	.
6 Aug.	.	.	.	.	.	.	.
23 Aug.	.	.	+	.	.	.	.

THE FOOD OF PIKE, *ESOX LUCIUS* L., IN WINDERMERE

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(With 7 Figures in the Text)

INTRODUCTION

A note on the food of pike in Windermere, based on 103 specimens caught between 1933 and 1935, has been published by Allen (1939). His fish were caught in seines during all months of the year and ranged from 15 to 100 cm. in length, the majority being 30–65 cm. long. From 1940 to the present day many more pike have been caught in Windermere, and by various methods, so that more detailed information on the food of pike of all sizes is now available. The present paper gives the results obtained from the examination of some 3000 fish from 1·5 to 105 cm. long, caught from 1940 to 1953, and deals with the food and feeding habits of the pike and the relationship of these to other fish in the lake.

The pike were taken from both north and south basins of Windermere. The lake has an area of 5½ square miles (14 sq.km.) and a mean depth of 70 ft. (22 m.) and the water is essentially soft. The fish in Windermere, in addition to the pike, are salmon (*Salmo salar* L.), brown trout (*S. trutta* L.), char (*Salvelinus willughbii* (Günther)), perch (*Perca fluviatilis* L.), eel (*Anguilla anguilla* L.), Stickleback (*Gasterosteus aculeatus* L.), bullhead (*Cottus gobio* L.) and minnow (*Phoxinus phoxinus* (L.)). Formerly the association of species was mainly trout and char, but since the eighteenth century environmental conditions have been more favourable to pike and perch, although the former are still important species in the lake. The experiment carried out by the Freshwater Biological Association, and still in progress, to reduce the perch and pike populations of Windermere (Worthington 1949) produced much of the material on which the present study of the food of pike is based.

MATERIAL

The pike examined were caught by standard seine, minnow seine, gill-nets and hand-net. Each year from April to September a seine is fished monthly in the north basin of the lake. The standard seine used is 50 yd. (46 m.) long and 12–15 ft. (3·7–4·6 m.) deep. The mesh is graded from 1 in. (2·5 cm.) knot to knot on the wings to ⅜ in. (0·9 cm.) at the bag. A minnow seine of 30 yd. (27·5 cm.) long was used specifically to catch smaller pike (particularly those of less than 20 cm.) which had a mesh of ¼ in. (0·6 cm.) knot to knot. This was used, particularly in weedy localities, from June to October, at various times during 1943 to 1951.

The removal of the pike in Windermere, in connexion with the experiment with fish populations being carried out in this lake, was done by means of gill-nets set during the winter and spring (October to March) from 1944 to the present day. The gill-net used consisted of a sheet of netting of 5 in. mesh (2½ in. knot to knot) of fine

twine and weighted to sink. The net 9 ft. (2·7 m.) deep and 30, 60, or 120 yd. (27·5, 55 or 100 m.) in length is usually set at right angles to the shore from shallow (6 ft. 1·8 m.) into deep water (25 ft., 7·6 m.) and is lifted two or three times a week. The nets, set at suitable places round the shore of the lake, are examined two or three days after each netting. In 1952 similar gill-nets were set, at a few of the winter netting stations, from April to September, inclusive, so that the food of the pike so caught might be compared with that of fish taken by seines during the same summer period and by gill-nets during the winter.

Table 1. *Length-frequency distributions of 3060 pike caught by different nets*

	Hand-net, May to June	Minnow seine, June to October	Standard seine, April to September	Gill-net, October to March	Gill-net, April to September
mm. groups					
10·5–12·9	73	—	—	—	—
13·0–17·5	33	—	—	—	—
1·0 cm. groups					
2·0–2·9	2	—	—	—	—
3·0–3·9	6	7	—	—	—
4·0–4·9	1	17	—	—	—
5·0–5·9	—	18	—	—	—
6·0–6·9	—	21	—	—	—
7·0–7·9	1	9	—	—	—
8·0–8·9	—	7	3	—	—
9·0–9·9	—	1	2	—	—
5·0 cm. groups					
10·0–14·9	—	16	21	—	—
15·0–19·9	—	13	26	—	—
10·0 cm. groups					
20–29	—	9	44	—	—
30–39	—	11	62	—	—
40–49	—	—	41	8	1
50–59	—	—	37	198	11
60–69	—	—	22	1348	74
70–79	—	—	6	508	27
80–89	—	—	—	215	8
90–99	—	—	6	119	1
100–105	—	—	—	27	—
Total	116	129	270	2423	122

A long-handled pond net with a fine muslin bag, the type used for the capture of aquatic insects, was used to catch the newly hatched fry and pike of 0·7–4 cm. long. Sweeps of this net were made in May, June and July, in or near Wray Castle boat-house dock and similar weedy places.

The results given in this paper are based on the examination of 3060 pike. Of these 270 were caught by seine, 129 by minnow seine, 2545 by gill-nets (2423 in winter, 122 in summer) and 116 by hand-net. The pike examined ranged from 0·7 to 105 cm. in length, and the length-frequency distribution of those taken by the different nets is given in Table 1. The length-frequency distribution of those fish giving results from pike of less than 20 cm. long is apparent from Table 2, and of more than 20 cm. from Table 5. Results are related throughout to length and not to weight, but so that they

may be interpreted in terms of the weight of the fish the lengths of 150 pike, ranging in length from 14 to 100 cm., have been plotted against the weights of the same individuals on a log–log scale (Fig. 1), and two best fitting straight lines have been drawn by eye, through the points: one fits fish of less than 2000 g., the other those over 2000 g. and the weight of the average pike of any given length may be read from these lines.

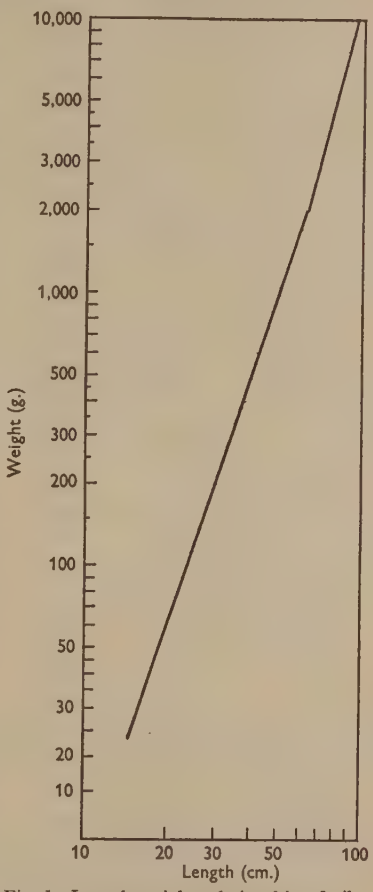

Fig. 1. Length-weight relationship of pike.

The alimentary canal of the pike consists of a U-shaped stomach and a short straight intestine. For fish of 20 cm. and less in length the whole alimentary canal was examined, as the small organisms were recognizable in the intestine as well as in the stomach, but for fish of 20 cm. long and over only the contents of the stomach were noted, those of the intestine usually being too much digested to be identified.

The food organisms were counted individually and identified, most of the invertebrates to the genus only, the vertebrates (fish) to species; fragments of fish were sometimes identifiable to species and when not so it was usually possible to distinguish those which belonged to non-salmonid groups. Many of the fish in the stomachs were measured, accurately or approximately, according to their state of digestion.

The stomach contents were recorded as the number of pike containing each food organism (frequency of occurrence) and the number of each organism present in the stomach. This last was seldom used in analysing results from large pike since the number of food organisms (fish chiefly) in a stomach was usually so low that such data gave little more information than was obtained from frequency of occurrence records. In presentation of results obtained from pike of over 20 cm. long the percentage figures for frequency of occurrence are based on the total number of fish examined, not only on those which contained food, and the same applies to figures of average numbers of organisms eaten.

RESULTS

The pike examined for food have been divided into two main groups, small pike, namely those of less than 20 cm., and large pike, those of 20 cm. and over.

(*a*) *Food of small pike*

There are 277 pike of less than 20 cm. long, and since this length covers their first year of life they are considered together to show the feeding for the period. In the

month of May (1945, 1950, 1951) 116 pike of 7·0–17·5 mm. were caught by hand-net in the dock leading into Wray Castle boathouse; the smallest specimens were taken in the weeds, the larger alongside the masonry of the dock wall. For June to September, in various years, 116 pike of 25–200 mm., 109 taken by minnow seine, and fifty-two by standard seine, were caught, the smaller fish in shallow weedy places, the larger in more open water. Of these fish, four were 7·0–9·0 mm. long and were newly hatched (in May), those of 10·0–17·5 mm. would be from 2 days to 4 weeks old, those up to 40 mm. about 6–8 weeks, and the remainder anything up to 4 months. The yolk-sac was present in individuals of from 7 to 12·5 mm. long, being still very heavy in specimens of 11·5 mm., although out of seventy-seven of 7·0–12·5 mm. there were eleven fish, including two of 11·0 mm., which had lost their yolk-sacs; Hunt & Carbine (1951), who examined small pike from drainage ditches which enter Houghton Lake, Michigan, also record two of this size as having no trace of yolk. In fish of 12–12·5 mm.

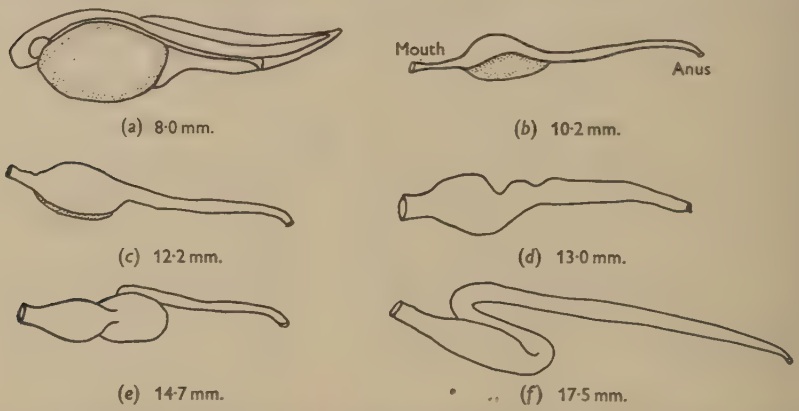

Fig. 2. Development of the alimentary canal in pike fry. The six main changes in shape taking place from that in newly hatched specimens 8·0 mm.) to that characteristic of adult fish at 17·5 mm. are shown. Yolk is indicated by stippling.

the yolk is present in varying amounts (nine out of thirty-five fish of this size range had lost their yolk altogether), and in all fish 13·0 mm. and more in length the yolk-sac had been absorbed; Hunt & Carbine (1951) record that at 12·0 mm. ten individuals had and four had not yolk-sacs, but Wurtz's (1945) observations suggest that the yolk-sac persisted on his fish until they were 14·0 mm. long.

Young pike can feed while there is still a considerable amount of yolk, for of sixty-two fish of 10·5–12·5 mm. there were twenty with yolk that had taken food. Hunt & Carbine (1951) remark that young pike 'may start feeding before the yolk is completely absorbed' but Wurtz's (1945) aquarium specimens did not begin to feed until the yolk was absorbed. The newly hatched pike of 7·0–9·0 mm. cling to some object; those I watched clung to the sides of the dish, and Balfour-Browne (1906) and Wurtz (1945) noted them clinging to vegetation in their aquarium. Both these authors find that this clinging period lasts about 8 or 9 days, Wurtz indicating that it is during the time of absorption of the yolk-sac; the little fish may let go their hold and dart about if disturbed (Balfour-Browne 1906). At the end of this period, by which time

Table 2. *Food of small pike (200 mm. long) given as the percentage frequency of occurrence of each food organism in different length-groups*

Food organism	Length-groups of pike in mm.											All fish
	10·5–12·9	13·0–17·5	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–149	150–199	10·5–199
Perca fluviatilis	—	—	—	54·0	67·0	83·0	71·5	70·0	40·0	—	29·8	23·0	34·8
Phoxinus phoxinus	—	—	—	15·5	5·5	—	—	—	30·0	66·0	40·5	51·0	18·7
Gasterosteus aculeatus	—	—	—	—	—	—	—	—	—	—	—	2·6	0·4
Fish fragments indet.	—	—	—	7·8	—	—	—	—	20·0	—	—	—	1·3
All fish	—	—	—	69·0	72·0	84·0	71·5	70·0	80·0	66·7	62·7	70·0	
Triton vulgaris (larval)	—	—	—	—	—	5·5	4·7	—	—	—	—	—	1·3
Aquatic insect larvae	—	—	100·0	30·8	16·7	11·2	38·0	20·0	20·0	33·3	16·2	10·3	14·8
Asellus and *Gammarus*	—	—	—	—	16·7	5·5	9·5	10·0	10·0	—	10·8	5·1	6·1
Bosmina	22·8	48·5	—	12·5	—	—	—	—	—	—	—	—	10·4
Chydorus	74·0	33·3	—	—	—	—	—	—	—	—	—	—	14·8
Eurycercus lamellatus	3·2	6·0	—	38·5	66·6	11·2	19·0	10·0	20·0	—	5·4	—	13·5
Other Cladocera	6·4	18·2	100·0	23·0	11·0	5·5	—	10·0	—	—	—	—	7·4
Cyclops	19·4	85·0	—	23·0	—	—	—	—	—	—	—	—	15·7
Other Copepoda	3·2	15·2	—	—	—	—	—	—	—	—	—	—	2·6
All Entomostraca	100·0	100·0	100·0	61·5	78·0	16·7	19·0	10·0	—	—	5·4	—	
Total fish examined	73	33	2	13	18	18	21	10	10	3	37	39	277
Percentage feeding	42·5	94·0	100·0	100·0	100·0	100·0	95·0	90·0	100·0	100·0	86·5	84·6	83·0

the fish are according to Wurtz (1945) about 14 mm. and to Balfour-Browne 11–13 mm., the fish become active and feed voraciously. The smallest feeding fish I took in Windermere was 10·5 mm. long; the majority of the very small feeding specimens were 12–12·5 mm.

The feeding habits of the small pike soon resemble those of the adult for, poised almost motionless, they suddenly dart upon their prey. This prey must be living and lively as Wurtz (1945) demonstrated. The alimentary canal shows changes in form with the growth of the fish (Fig. 2), developing from a straight tube to the S bend form of the adult by the time the fish is 17·5 mm. long; Wurtz (1945) states that the anus opens to the exterior when the fish is 11·5 mm.; in my feeding specimen of 10·5 mm. the anus was open.

The food of the 277 small pike is given in Table 2 where the frequency of occurrence of a food is shown as a percentage of the number of fish examined, both feeding and empty, except for group 10·5–12·9 mm., in each length-group. For these fish of 10·5–12·9 mm. the percentage is based on feeding fish only since the forty-two empty fish had yolk and were probably empty for that reason and not because they were fasting fish; of the thirty-one feeding fish in this group twenty were carrying yolk.

The foods eaten are divided into twelve individual and two collective categories. The larval aquatic insects include Ephemeroptera nymphs, chiefly *Cloëon* sp. Chironomid larvae and pupae, Odonata nymphs, and Trichoptera larvae. The specimens of *Bosmina* identified were *B. obtusirostris* Sars and those of *Chydorus*, *C. sphaericus* (O.F.M.). The group 'Other Cladocera' included *Sida crystallina* (O.F.M.), *Ceriodaphnia pulchella* Sars, *Daphnia* sp., *Alona* sp. and *Leptodora kindti* (Focke). Some of the Cyclops eaten were identified as *C. macruroides* (Lilljeborg), the 'Other Copepoda' were *Diaptomus* and Harpacticoida.

Table 2 shows that Entomostraca, larval aquatic insects and fish are the three main food items, and Fig. 3 their relative importance to pike of different sizes. The Entomostraca are the only foods found in fish of 17·5 mm. and less, and continue to be important up to 50 mm. after which their incidence in stomachs diminishes. Insect larvae first occur in the diet when the fish are 25–29 mm. long, and although they are found subsequently in all sizes of fish they are never of primary importance. Fish enter the dietary when the pike are 35 mm. long, they are then an important part of it and remain so thereafter (Fig. 3). The food of pike of 11·0–15·2 mm., as shown by Hunt & Carbine (1951), also consisted of Entomostraca, aquatic insect larvae and fish, which groups in spite of some overlapping in the feeding habits, form a feeding sequence as the pike increase in size, but in Windermere such a sequence is more from Entomostraca to fish, as the insect larvae are eaten contemporaneously with fish. The difference in importance of insect larvae in these two waters may be associated with their relative abundance in the two places, for such larvae would probably be more common in the weedy drainage ditches of Houghton Lake than in the bays of Windermere.

The importance of Entomostraca to young pike is evident from their being the only food of fish of less than 17·5 mm. long, where also they have high figures for frequency of occurrence. Table 2 shows that on the whole Cladocera are more frequently eaten than Copepoda, and that the incidence of the latter is greater in the larger (13·0–17·5 mm.) than the smaller (10·5–12·9 mm.) fish; this may be because the smaller fish found

Cyclops difficult to catch, as Wurtz (1945) noted for his aquarium-reared pike. The Cladocera *Bosmina* and *Chydorus* are found only in the very small pike, and among them *Bosmina* is more frequently eaten by the larger and *Chydorus* by the smaller specimens; both are small species. On the other hand, the occurrence of *Eurycercus lamellatus* (O.F.M.), a large cladoceran, shows some increase in frequency with the increase in size of the pike, and the 'Other Cladocera' which are large species show no definite trend in frequency of occurrence with the size of the fish. The number of Entomostraca found in any individual pike was never greater than seventeen *Cyclops* and three *Chydorus* in one fish (14 mm.); in most cases it was less than ten. Hunt & Carbine (1951) found far greater numbers of these organisms in fish of the same size. The

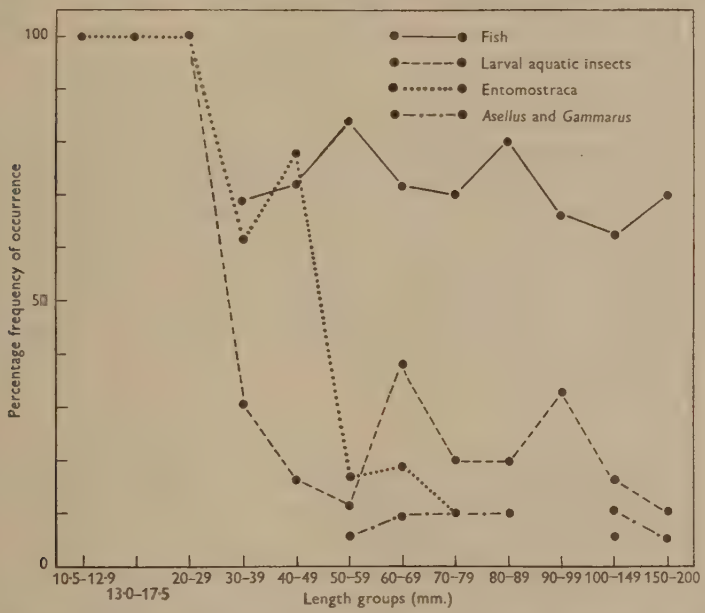

Fig. 3. Percentage frequency of occurrence of each of four groups of food organisms in pike of different length-groups.

Entomostraca found in the stomachs are, apart from the one occurrence of *Leptodora*, weed-living species. For his study of the food of perch fry Smyly (1952) made zooplankton collections from Wray Castle boathouse, the site of capture of many of my small pike, particularly those of 10·5–17·5 mm. His collections indicate abundance of these weed-living Entomostraca, particularly in May and June, so that there is no lack of food for the small pike. A similar abundance of food for young pike was noted by Montén (1950) for 'an enormous food surplus was observed at the spawning grounds, about 400 *Bosmina* units per liter'.

Larval aquatic insects considered collectively showed no high frequency of occurrence (apart from the two 25–29 mm. fish) and the maximum number in any one fish was nine. Of the different insects present the chironomid larvae and pupae occurred in thirteen, Ephemeroptera nymphs in ten, Odonata nymphs in six, and Trichoptera

larvae in three of the pike respectively, which numbers perhaps reflect their relative proportions in the fauna. Larval insects, which played a much more important part in the diet of pike up to 60 mm. long examined by Hunt & Carbine (1951) consisted principally of larval and pupal Chironomidae.

Fish are by far the most important food of the pike from 35 mm. onwards (Fig. 3). From this size to 90 mm. they feed almost entirely on perch fry of 10 to about 20 mm. long, which are present in large numbers in the sheltered shallow bays of Windermere in late May and June. 'During the summer the perch fry grow from 40 to 60 mm. in length' (Smyly 1952), and at this size they are the food of the pike of 140–200 mm. These perch fry, particularly the smaller ones, must be an almost unlimited food supply for the growing pike and provide an abundance of larger food organisms just at the time when the young pike is increasing rapidly in size and requiring such food. The same increase in size of prey with the increase in size of predator is found also among the minnows eaten, for the pike of 30–50 mm. eat specimens of about 10 mm. in length, whereas those of 120–200 mm. take the 20–50 mm. specimens. Sticklebacks are negligible in the diet. There is no record of cannibalism among these small pike of Windermere, whereas forty out of 203 pike examined by Hunt & Carbine (1951) in 1939 contained the young of their own species, and these authors consider that such cannibalism is an important factor in reducing the population of pike. Montén (1950), on the other hand, notes that there was no cannibalism in Nature, but in stew ponds 'if the population is dense cannibalism will often result [appearing first in fish of 25 mm.] if there is insufficient food'. Wurtz (1945), in his observations on his aquaria fish, mentions cannibalism as 'de rigeur' among the fish 3 weeks after they were hatched.

The remaining foods of the diet show no high figures for frequency of occurrence. The larger crustacea are eaten by the larger of the small pike, although *Gammarus* occurred in three fish only, whereas *Asellus* was eaten by all; probably the latter were the more accessible. The only remarkable feature of the diet of the small pike was that a specimen of 62 mm. had eaten thirteen larval newts.

The feeding of the small pike covers the months of May to September, during which time the fish grew from 7·0 mm., the size at hatching, to as much as 200 mm. in length so that any seasonal changes in the diet cannot be dissociated from those associated with the rapid change in form and size which occur during the fish's first few months of life.

(*b*) *General features of the food of large pike*

There were 2783 pike of 20–105 cm. long, termed large pike, examined for stomach contents. Of these fish (caught from 1941 to 1953) 218 taken by standard seine, twenty by minnow seine, and 122 by summer gill-net were caught from April to October so that collectively the 360 specimens are termed summer caught and classified as 'seine'-caught since the majority were so captured and because the results of those fish taken in summer set gill-nets were similar to those seined. The remaining 2423 pike taken in gill-nets set from October to March represent winter-caught pike. It is apparent from Tables 1 and 5 that, although there is some overlapping of size, the majority of the seined fish are smaller than the gill-netted; the possibility of this affecting the results has been borne in mind.

A general picture of the food of the 2783 large pike based on all the data is shown in Table 3 and includes the frequency of occurrence of each food category in the 360 seine- and 2423 gill-netted pike; for these combined data are given. The diet is almost entirely one of fish, with perch, trout and char as the main species eaten. Perch and trout appear to be equally important as foods, but the seine-caught pike stress the

Table 3. *Food of large pike (20–105 cm. long): the frequency of occurrence of each food organism in total fish examined (these figures as percentages are in parentheses), and the average number eaten per fish*

	Number of pike eating each food. Pike caught by			Average number of each food organism eaten. Pike caught by		
FOOD ORGANISM:	Seine	Gill-net	Combined nets	Seine	Gill-net	Combined nets
Perca fluviatilis (perch)	118 (32·8)	211 (8·7)	329 (11·8)	0·63	0·14	0·37
Salmo trutta (brown trout)	9 (2·5)	315 (13·0)	324 (11·6)	0·027	0·15	0·09
Salvelinus willughbii (char)	1 (0·03)	479 (19·7)	480 (17·2)	0·001	0·21	0·11
Gasterosteus aculeatus (three-spined stickleback)	22 (6·1)	84 (3·4)	106 (3·8)	0·17	0·16	0·16
Phoxinus phoxinus (minnow)	31 (8·6)	17 (0·7)	58 (2·1)	0·11	0·05	0·08
Esox lucius (pike)	5 (0·14)	28 (1·1)	33 (1·2)	0·02	0·01	0·01
Anguilla anguilla (eel)	2 (0·05)	3 (0·1)	5 (0·2)	0·01	0·001	0·005
Salmonid fragments	3 (0·08)	64 (2·6)	67 (2·4)	0·025	0·02	0·02
Fish fragments indet.	11 (3·0)	133 (5·5)	144 (5·2)	0·02	0·05	0·03
Invertebrate bottom fauna	9 (2·5)	4 (0·1)	13 (0·5)	0·03	0·003	0·02
Total no. fish examined	360	2423	2783	360	2423	2783
Percentage feeding	52·7	51·9	52·0	52·7	51·9	52·0

greater importance of the perch. The high contribution of char, although a seasonal effect (p. 348), is most marked. Of the other species of fish in Windermere the stickleback and the minnow are eaten to some extent; the frequency of the former in the stomachs is higher than that of the latter. Cannibalism is negligible and the eel is of no consequence as a food. The invertebrates of the diet, Ephemeroptera and Plecoptera nymphs, Trichoptera larvae, *Asellus*, *Gammarus* and molluscs occur to some small extent in the stomachs of seined pike, but fish predominate, a predominance in seine-caught pike also shown by Allen (1939). His results show also 'predominance of the perch' over all other fish in the diet, with the trout of minor importance, and sticklebacks and minnows as appreciably more important than the trout. The relative importance of the different species of fish is more clearly defined when the results obtained from the stomach examinations are considered in relation to the season of capture and size of the pike.

(*c*) *Seasonal food*

The food of the pike in different months of the year is shown in Table 4 and Fig. 4, in which data from all fish of 20 cm. and over are given as the number of pike containing each type of food expressed as percentages. To obtain these percentages the frequency of occurrence of each food for each month for each 10 cm. length-group was found; the figure so obtained was then expressed as a percentage of the total

number examined and then these percentages were added together for any one month and divided by the length-groups contributing to that month. In this way the effect of the variation in the numbers of fish examined each month was minimized.

Seasonal differences in the diet may have been affected by the difference in method of capture, the pike of October to March being gill-netted, those of April to September being seine-netted. This difference also affected the size of the pike caught, the gill-net catching the larger fish, and an attempt to see the effect of this was made in 1952 when gill-nets were used from April to September contemporaneous with the seine-nettings. The gill-nets did catch larger pike, but stomach contents of these fish showed no qualitative difference from the seine-netted specimens taken at the same period.

Table 4. *Seasonal food of pike: percentage frequency of occurrence of each food organism in total fish examined for each month*

Month ...	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Perca fluviatilis	8·2	6·6	18·0	9·2	50·6	58·7	57·3	30·5	40·2	22·8	5·9	3·5
Salmo trutta	20·8	20·2	6·2	0·3	4·0	—	3·0	4·6	3·1	14·6	7·8	10·8
Salvelinus willughbii	9·0	5·2	6·7	—	—	—	—	0·9	—	11·2	47·8	27·4
Gasterosteus aculeatus	3·4	1·2	1·0	1·5	14·1	12·9	39·0	1·7	—	—	2·1	2·3
Phoxinus phoxinus	0·5	0·7	—	1·0	6·5	9·6	4·1	6·0	13·3	0·6	0·8	0·2
Esox lucius	0·4	1·2	0·4	—	6·1	—	4·3	—	1·4	1·2	0·8	0·5
Anguilla anguilla	0·4	—	—	—	—	—	—	—	7·7	—	0·7	—
Salmonid fragments	3·0	2·0	15·6	0·5	—	—	—	—	4·7	3·1	2·7	1·9
Fish fragments indet.	—	—	—	1·3	4·2	2·7	1·1	3·7	—	4·2	3·8	—
Invertebrate bottom fauna	—	—	2·4	—	6·4	1·3	—	—	1·9	1·2	0·2	—
Total no. fish examined	465	469	133	101	52	49	52	66	49	159	587	601
Percentage feeding	45·2	40·3	43·0	14·8	82·7	71·4	61·5	53·0	65·3	54·0	65·7	54·9

No seine-nettings were taken from October to March, contemporaneous with the winter gill-nettings, but seine-nettings taken by Allen (1939) during this period show that the diet of his fish was much the same as that of fish taken by me in the gill-net except for the noteworthy exception of char.

Table 4 and Fig. 4 show that throughout the year perch are important to the pike, especially from May till September when they are by far the most important of all foods, a fact which is associated, no doubt, with the presence of the perch in the shallower water during spring and summer months. In October perch are still common in the diet, but after that few are eaten, a reflexion of the deep-water habitat of these fish during winter and early spring. Char are the main food in November and December when the figures for the frequency of occurrence are higher than those recorded for any food, except perch. The time and extent of this predation is coincident with the availability of the char, for in November and December there is a population of char in Windermere which comes into the shallows to spawn (Frost 1951) and such congregations of breeding fish (and all the char taken from the pikes' stomachs were spawners) are easy prey for the pike. The number of individuals found in the pike ranged from one to three. Allen (1939) found no char in the 103 seine-caught pike taken throughout the year, of which thirty-two were caught from November to March, and concludes that, as the pike is largely confined to the littoral regions of Windermere, the habit of the char of being in the open deep water except during the autumn

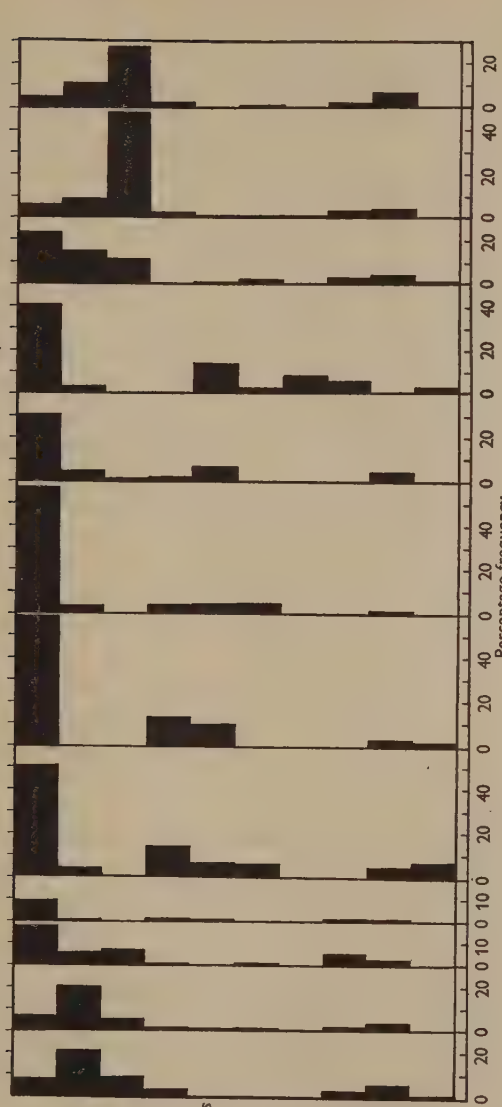

Fig. 4. Percentage frequency of occurrence of each food organism in total pike examined each month.

spawning time, made it 'hardly available' as food. The predation now recorded was revealed by the use of the winter set gill-nets the settings of which, being far more numerous, resulted in a much more complete sampling of the pike, both in time and space, than was possible by the occasional seine haul previously carried out. Char are eaten to some extent from January to April, and again almost all these are breeding fish since they belong to the population of Windermere char that spawns in February and March. The site of this spawning, however, though close inshore is in deep water (60–100 ft.) so that the char congregated on such spawning grounds are away from the littoral haunts of the pike which presumably would prey only on those char that strayed into shallower water on their way to the spawning place. For the rest of the year the char is wholly free from attack. In marked contrast to the periodicity of this predation, the feeding on char by pike in Thirlmere (10 miles to the north of Windermere) may be mentioned. Here for the 148 pike, mostly 68–72 cm. long, caught from May 1952 to February 1953, the main food was char, which occurred in 75% of the fish and were present in every month; perch and trout were seldom eaten. From specimens found in the stomachs of pike taken in gill-nets and in seines the char of this lake appear to be small, 17–20 cm., and slow-growing. Nothing is known of their habits, except that in spring and summer they could be netted in shallow water near the shore and in July they were so near the surface and close inshore that they were caught by rod and line fished from the bank. These captures show that the availability of this prey explains the pike's feeding on them in spring and summer in Thirlmere, but as the location and habits of the char in autumn and winter are unknown the reason for predation on them at this time remains to be found.

The consumption of brown trout is highest from October to February which is probably, in part at least, also associated with the breeding habits of this fish, since from October to December the trout are likely to be in or near shallow water as they make their way to the rivers to spawn; many of the trout eaten were breeding fish. Trout would be available from March to June as they are then in shallow waters of the lake; they may, however, have been safe from predation because the pike could at this time find an abundance of perch. The low consumption of trout in the months June to September is probably because this fish usually leaves the shallows in late June. Sticklebacks, although at no time of great importance as food, are eaten mainly in May and June, at which time they congregate for breeding. In Windermere minnows spend the winter under stones and are therefore free from predation, but from May onwards they lose this immunity when they live in shoals in the littoral zone. Cannibalism, never very marked at any time, shows little seasonal variation in intensity. Eels, probably owing to their non-gregariousness and bottom-living habits are seldom eaten at any time of year.

The invertebrate bottom fauna at all times contributed very little to the diet; the maximum frequency of occurrence, in May, was chiefly due to larval aquatic insects, although a few *Gammarus* and *Asellus* were also eaten. This virtual absence of invertebrates in the food is in contrast to the high frequency with which *Gammarus* occurs in pike (of 20–46 cm.) caught in April and May in Danish streams, where the pike appears to be a serious competitor with trout for this food (Larsen 1951).

The changes in the character of the diet of the pike in Windermere throughout the

year are almost entirely governed by the availability of the fish food species which is an expression of the seasonal changes in habit of the different fishes. There seems to be little evidence of seasonal selection of species by the pike unless comparison of the frequencies for trout and perch for December to March, particularly those for February, suggests a selection of trout, for it is likely that both species of fish are equally available in these winter months.

(*d*) *The food of pike in relation to size*

Changes in the diet of pike of less than 20 cm. long have been discussed (p. 343). Pike of more than 20 cm. long (20–105 cm.) have been divided into 10 cm. length-groups and the food of each group of fish is shown in Table 5 and Fig. 5. The results have been obtained for each length-group by taking the percentage frequency for each month found for a length-group, totalling these frequencies and dividing the result by the number of months contributing to the particular group. In this way the effect of the wide range in the number of fish examined in the different length-groups has been minimized. The effect of the method of capture is seen in that all except eight of the fish of less than 50 cm. long were seine-netted (which also means that they were taken from April to September) and that the fish which were gill-netted, and therefore winter caught, were over 50 cm. long and far more numerous than those of this length taken by seine. However, results from the two sets of data combined show that method and time of capture do not materially affect the differences found in feeding of pike of the different length-groups.

Perch, the fish most frequently eaten, are important in the diet of all fish less than 80 cm. long, and they rise steadily to a maximum value in fish of 50–59 cm. Brown trout, although eaten by pike from 20 cm. long, become a significant part of the diet in pike 40 cm. and more in length, and show only little variation in this significance with increase in size of the pike. The char, of greatest frequency of occurrence in the pike of 50–59 cm., occurs to much the same extent in larger fish; since there are no char in the summer-caught fish they are also absent from the diet of the pike less than 50 cm. long. The occurrence of sticklebacks is appreciable in the diet of pike of 30–59 cm., being highest in the 50–59 cm. length-group, but their incidence in larger pike is very low. Minnows, which are of most importance to pike of 20–29 cm. (much more so than sticklebacks), cease to be of any significance in the diet of those more than 50 cm. long. Cannibalism, which plays only a small part in the feeding of pike of all sizes, shows perhaps some tendency to occur more in the smaller (20–29 cm.) and larger (70–79 cm.) individuals than in the rest; possibly the former is associated with the smaller fish being more numerous than the larger. Eels are so seldom eaten that their occurrence can show no relationship to the size of the pike eating them. The invertebrate bottom fauna, never eaten to any marked extent, shows the highest frequency of occurrence in the smallest length-group where the organisms eaten were larval Odonata, Ephemeroptera nymphs and *Gammarus*.

These data demonstrate, to some extent, the principle illustrated by the perch of Windermere (Allen 1935) that as the fish increases in size there is an increase in the size of the animals which it eats. In the perch this was brought about by a change in the kind of foods eaten, and the same applies to pike less than 20 cm. long, but for

larger pike, since their diet is mostly fish, the principle is demonstrated through the differences in size of the fish species. Thus the two small species eaten, stickleback and minnow, although eaten by pike 20–89 cm. long are chiefly the food of those of less than 59 cm., and minnows although making a great contribution to the diet of pike of 20–29 cm., contribute little or nothing to that of the larger fish. The perch,

Table 5. *Food of pike in relation to size given as percentage frequency of occurrence of each food organism in pike of different 10 cm. length-groups*

Length-group (cm.)	Food organisms: *Perca fluviatilis*	*Salmo trutta*	*Salvelinus willughbii*	*Gasterosteus aculeatus*	*Phoxinus phoxinus*	*Esox lucius*	*Anguilla anguilla*	Salmonid fragments	Fish fragments indet.	Invertebrate bottom-fauna	No. of fish examined	Percentage feeding
360 SEINE-NETTED PIKE (Apr.–Sept.)												
20–29	30·0	2·0	—	3·2	34·4	4·0	—	—	3·2	6·0	53	67·9
30–39	36·4	2·8	—	9·0	9·6	—	1·2	—	3·0	2·7	73	60·3
40–49	48·5	1·1	—	8·3	7·1	2·8	—	—	1·3	3·8	42	73·7
50–59	58·4	3·1	—	14·3	—	—	—	—	2·9	—	48	56·3
60–69	42·4	6·0	1·1	2·1	0·5	1·3	—	0·7	2·9	—	96	36·4
70–79	36·8	2·8	—	—	1·1	5·5	—	—	1·1	—	33	39·4
80–89	25·0	—	—	—	—	—	—	25·0	—	—	8	25·0
90–99	16·5	—	—	—	—	—	16·5	16·5	—	—	7	28·6
2423 GILL-NETTED PIKE (Oct.–Mar.)												
40–49	40·0	20·0	—	10·0	—	—	—	—	—	—	8	62·5
50–59	15·4	16·7	30·0	2·0	1·0	1·0	—	2·5	1·2	—	198	66·7
60–69	13·9	10·4	16·0	3·1	0·89	0·8	0·04	4·4	1·4	0·9	1348	51·4
70–79	4·3	12·2	12·2	1·3	0·1	0·1	—	4·5	4·2	—	508	49·6
80–89	4·2	14·8	13·1	1·5	—	0·8	0·2	5·5	1·5	0·3	215	49·3
90–99	5·7	8·0	15·7	—	—	0·9	0·4	3·4	4·3	—	119	48·7
100–105	10·4	14·4	17·6	—	—	—	—	12·0	—	—	27	51·9
2783 PIKE CAUGHT BY BOTH TYPES OF NET												
20–29	30·0	2·0	—	3·2	34·4	4·0	—	—	3·2	6·0	53	67·9
30–39	36·4	2·8	—	9·0	9·6	—	1·2	—	3·0	2·7	73	60·3
40–49	44·5	9·4	—	9·0	4·0	1·4	—	—	0·7	4·0	50	72·0
50–59	33·0	11·8	15·4	9·5	0·6	0·6	—	0·8	3·6	—	246	64·6
60–69	42·4	9·5	8·9	3·0	0·2	0·5	0·02	1·1	4·2	0·2	1444	50·4
70–79	44·0	8·6	7·2	0·8	0·6	2·8	—	2·5	3·2	—	541	48·0
80–89	14·0	9·9	6·6	1·0	—	0·6	0·8	1·8	3·6	0·02	223	48·4
90–99	9·1	6·1	13·7	—	—	0·8	4·5	8·0	3·0	—	126	47·6
100–105	10·4	14·4	17·6	—	—	—	—	—	12·0	—	27	51·8

trout and char present species of different sizes, for the mean sizes of those eaten is 12·9, 29·4, and 28·0 cm. respectively for the three species. Among the first two there is a higher frequency of occurrence of trout than perch in pike over 70 cm. long, which suggests that the larger pike have chosen the trout as being the larger assuming that the trout and perch were equally available as food to these winter-caught pike. That all pike of over 50 cm. eat more char than perch is almost certainly not associated with the char being the larger fish, but rather with the great accessibility of the char during

the winter months when most of such pike were caught. Allen (1939) does not relate the fish species eaten with the size of the pike, but considers them collectively and finds that pike of more than 38 cm. tended to eat larger fish than did pike less than 38 cm. long since the mean lengths of the fish eaten by the former was 8·65 cm. and by the latter 6·02 cm. The increase in size of food associated with increase in size of

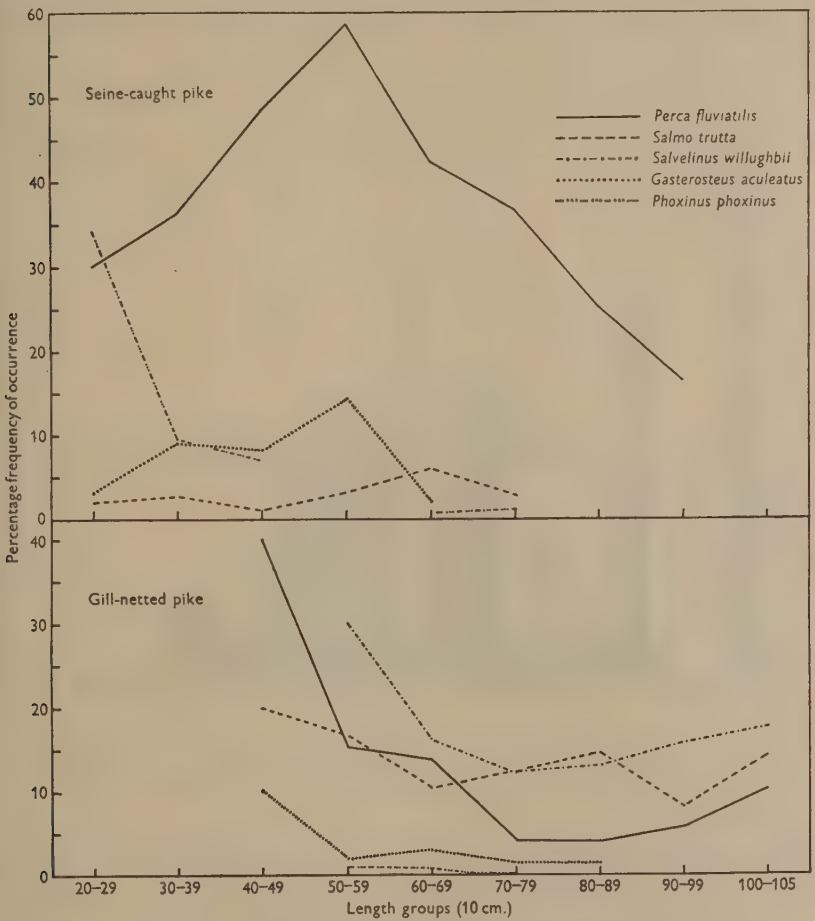

Fig. 5. Percentage frequency with which five species of fish occurred in diet of pike of different length-groups; pike caught by seine and gill-net shown separately.

the pike may be effected by a change in the choice of the size of the individuals of a species eaten; this has already been well illustrated by the different size of the perch and minnow eaten by the pike of less than 20 cm. The perch and trout found in the stomachs of large pike (20 cm. and over) include individuals of a wide range in size. Many of these fish were measured and the mean size for those eaten by pike of different length-groups was found. For the perch the mean size found in pike of

10 cm. length-groups was: 20–29, 6·1 cm.; 30–39, 9·3 cm.; 40–49, 10·3 cm.; 50–59, 12·6 cm.; 60–69, 12·8 cm.; 70–79, 13·7 cm.; and 80–99, 13·1 cm.; showing that the larger the pike the larger the perch on which it feeds. This conclusion is emphasized if the mean size of perch eaten by the 360 seine-caught (summer) pike is compared with that of the 2423 gill-netted (winter) pike, for the average size of the summer-caught pike is 60 cm. and that of the perch they eat is 10·28 cm., while the winter-caught pike of average size 67 cm. eat perch which have a mean length of 13·6 cm.

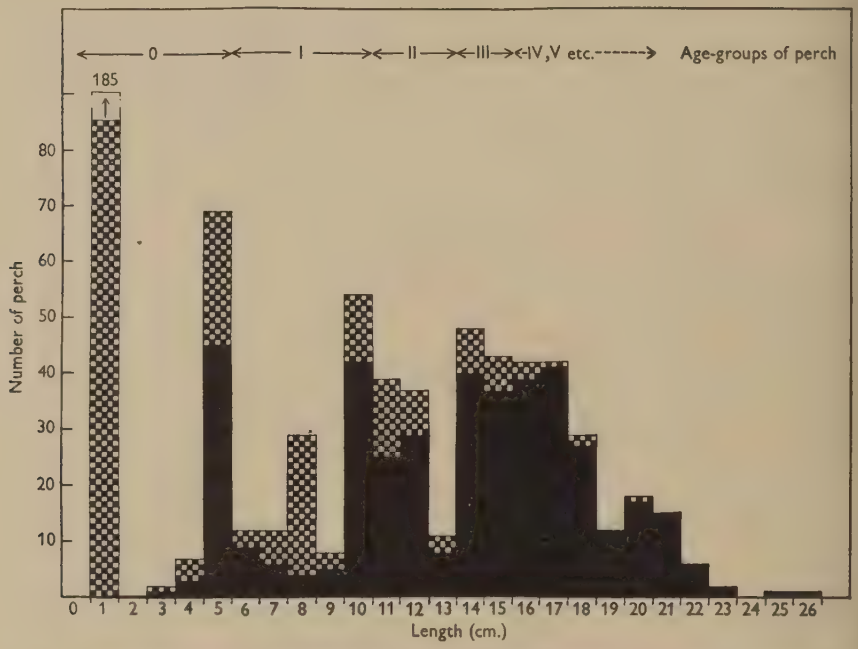

Fig. 6. Length-frequency of the perch taken from pike stomachs; data from gill-netted pike black, from seined pike, black and white; roman numerals show age-groups of the perch, these data from Le Cren (personal communication).

Fig. 6, which shows the length-frequency distribution of perch taken from pike stomachs, gives further information on this size relationship between predator and prey. The distribution represents very much the same size-range and age-groups as that of the perch population in the lake (Le Cren, personal communication) except that 0, I and II group fish are under-represented. The diagram indicates that the pike, although eating all sizes of perch, tends to select those of age-groups III and over, especially the larger pike of 60–70 cm. such as those caught in gill-nets. On the other hand, although there is heavy cropping of the newly hatched perch, the 0, I and II group fish are not eaten by the pike, relative to the older perch, in proportion to their abundance in the lake.

Only twelve trout were found in the stomachs of pike taken in seine-nets and these

were not measured, but of the many in the stomachs of gill-netted pike the 352 measured had a mean length of 29·5 cm.; the mean size of the trout in each of the 20 cm. length-groups of pike was as follows: 50–59, 25·9 cm.; 60–79, 29·4 cm.; 80–99, 31·9 cm.; and 99–105, 43 cm. (the last figure based on five fish only). Again the increase in length of the predator is associated with an increase in that of the prey. Fig. 7 shows the length-frequency distribution of these trout, and also the length-for-age of the trout and the estimated number of trout in each age-group, these latter data being based on Allen's (1938) results. From comparison of the three types of data it may be concluded that the pike select the larger and the older trout. The much less heavy predation on the younger and smaller fish is chiefly on those of

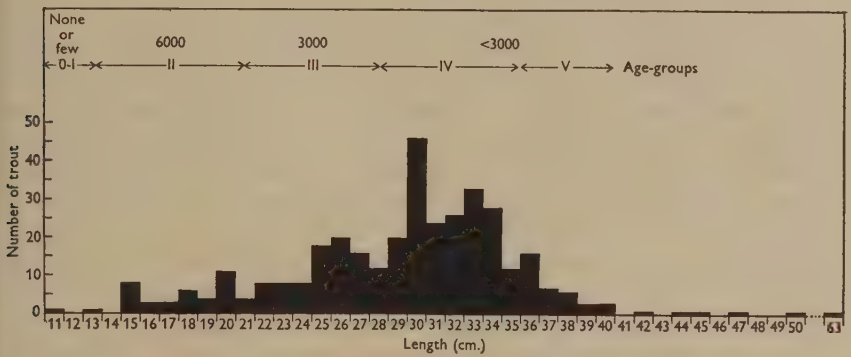

Fig. 7. Length-frequency of the trout taken from pike stomachs. The length for age relationships of the trout are shown by roman and the numbers of fish in each age group by arabic numerals; these data based on Allen (1938).

the II group, as would be expected since few trout enter the lake before they have completed 2 years of river life. Predation on large trout is almost entirely by the big pike (60–70 cm.); the smaller pike eat few trout (Table 5) even though smaller ones are known to be quite common in the lake.

The char eaten by the pike were mostly from 27 to 30 cm. long, the size-range of the autumn-spawning population; such fish were 5–8 years old. As the predation by the pike was confined to these breeding fish, selection for size of prey was precluded, and as pike of all sizes between 40 and 105 cm. eat the char predation was not limited to any particular size of predator.

For the minnow the evidence from small pike (20 cm. and less) shows that the larger the pike the larger the minnow on which it feeds.

As for the pike's feeding on its own species the newly hatched and young fry seem to be immune from attack. The size of any pike eaten is seldom greater than 40 cm., and as such fish are usually less than 3 years old the pike apparently selects the smaller and younger members of the population.

(*e*) *Feeding and fasting*

It is known from pike confined in artificial waters that the fish can survive long periods of starvation, and it is a popular belief that periodic abstinence characterizes

its feeding habits. I have no scientific evidence for the latter but some information on fasting may be derived from the data on numbers of stomachs with and without food.

In Tables 2–5 the number of pike containing food is shown as a percentage of the total fish examined. Of the 277 pike less than 20 cm. long (Table 2) 83% were feeding fish. Among these small pike fasting fish are confined to those less than 13 mm. long. That this is associated with the high proportion of individuals which carried yolk is evident from the fact that as soon as the yolk is gone fish but little larger in size (13–17·5 mm.) and with a similar diet are all feeding. The absence of fasting which characterizes small pike is doubtless related to their diet of small organisms, which because of their smallness require more time to collect in the larger numbers needed; there is thus less time for the stomach to be empty. The larger pike (20–105 cm.) show a proportion of feeding fish (52·7% Table 2) which is always lower than was found among the small pike. There is some tendency for the percentage of feeding fish to decrease with increase in the size of the pike (Table 5). This is particularly emphasized by the data for seine-netted specimens. All these results support the generalization that a high proportion of empty stomachs is a 'characteristic of fish-eating fish', since as Allen (1935) pointed out from his study of Windermere perch the large size of the foods eaten will enable the fish to 'obtain a large amount of food comparatively quickly, so that there may be an interval between each feeding period when its [the predator's] stomach will be empty'.

Seasonal variation in the intensity of feeding may be, to some extent, deduced from the proportions of feeding fish in the different months (Table 4). The method of capture may have affected the results given from October to February since these are based on gill-netted pike only and fish so caught, being held much longer in the net than if seine-netted, are more likely to have got rid of their food by vomiting or digestion than the seine-netted individuals of other months. The lowest percentage of feeding fish is found from January to April; the figures for January and February suggest a slowing down of feeding in these cold months, and the lowest of all, in March and April, are most probably indicative of a fast associated with spawning time. That the fast is real is supported by the fact that the results when seine- and gill-netted fish are considered separately are much the same. The high figure for feeding in May perhaps reflects the voracity of spent fish. If the data for all fish are divided into two periods November to March (winter) and April to October (summer), as Allen (1939) subdivided his data from seine-caught fish, it is found that 52·0% were feeding in 'winter' and 52·5% in 'summer', whereas Allen found 56 and 73% feeding fish for the two periods respectively and so emphasized the relatively fasting state of the pike in winter.

THE RELATIONSHIP BETWEEN PIKE AND OTHER FISH IN THE LAKE

This relationship, as defined by feeding habits, is determined to some extent by competition for food between the fish species but primarily by the pike's predation on other fish.

Competition for food, taken to mean the result arising from the food supply being insufficient in relation to the demands made upon it, may be a factor during the first

year of life as then the diet of the pike (Entomostraca and bottom-living invertebrates) is similar to that of some other fishes in the lake (Frost 1945). Since the period of feeding on Entomostraca is so short, and the supply unlikely to be poor, competition for them seems improbable but the longer time of predation on invertebrate bottom fauna and the heavy demand made on it by all fish species suggests that some competition for this may occur, but as the young pike is contemporaneously feeding on the abundant perch fry (on which there is no other predator except possibly some trout and large perch) competition, for food as such, among small pike is reduced and probably removed altogether.

Of the fish eaten by larger pike, perch, sticklebacks and minnows are also eaten by perch over 18 cm. long (Allen 1935) and by trout 40–70 cm. long (Frost, unpublished data), and at such sizes both species are almost entirely piscivorous. The fish diet of the perch consists mainly of minnows, to some extent sticklebacks and to a less extent of perch; that of the big trout is almost entirely perch, the other two species being seldom found in the stomachs. The overlapping of these requirements with those of the pike for the same species might lead to competition for perch and minnows but it seems unlikely that this would be so since the big trout and big perch form a relatively small proportion of the populations of these species and there is a great known abundance of perch and an apparent abundance of minnows in the lake. Moreover, the removal of large pike in the last ten years will have reduced the pressure of predation on the perch supply; although the trapping of perch which has been carried on in the lake since 1940 (Worthington 1949) has considerably reduced the number of this fish also (p. 358).

Some idea of the effect of predation on fish compared with their numbers in the lake is obtained by comparing the average number of each fish species eaten (Table 3) with their presumed relative abundance in the lake. In Table 3 the average figures for seine-netted (April to September) pike represent summer feeding, those for the gill-netted fish (October to March) winter feeding, and the combined data the overall predation. The perch is known to be the most abundant fish in the lake and the trout relatively much less numerous; the catch of fish in standard seine-nettings for April to September from 1945 to 1953 inclusive gave a ratio of 16 to 1 for the two species (Le Cren, personal communication). The average figures of 0·63 and 0·027 for the perch and trout eaten by seine-caught pike show much the same ratio, probably because both species of prey are in shallow water in spring and summer and so equally available to the pike. The identity of the average figures, 0·14 and 0·15 for perch and trout eaten by gill-netted pike, may be explained by the perch being less available than the trout in winter time, a factor which would offset its greater relative abundance and account for the trout being 'selected' by the pike. Char are perhaps as numerous as trout in the lake and so have the same relative abundance to perch. The high average figures for consumption of 0·11 for the rare char and 0·37 for the abundant perch can only be explained by the much greater availability of char in winter time, which is expressed in the average figures for gill-netted pike of 0·21 and 0·14. Of the small species eaten, the stickleback and minnow, the latter is according to Allen (1939) much the more abundant species in the lake. If this is so, the average numbers eaten, 0·16 for stickleback, 0·88 for minnow, show an inverse relationship to their relative

abundance in the lake. Since this relationship is maintained in both summer- and winter-caught pike, it cannot be accounted for by some seasonal difference in the availability of minnow and of stickleback, and it can only be suggested that the pike selects the stickleback. Pike are perhaps of the same order as trout in their relative abundance to perch in the lake but the average number of pike eaten is much below that of trout so that the pike population is cropped much less heavily than the trout. Eels, which are probably as numerous as pike in the lake, are eaten to an even less extent than the pike. Their inaccessibilty relative to that of other more abundant species is likely to be the factor that offsets their relative abundance. Finally the number of invertebrates must be infinitely greater than that of any fish and the relatively infinitesimal number eaten is an expression of the essentially fish-eating character of the pike.

In Windermere to-day the association of species is one of char, trout, pike and perch. It seems likely that in former times it was mainly represented by char and trout, but latterly the environment has become more favourable to a preponderance of perch particularly and also to pike (Worthington 1949). Since 1940 an attempt to alter this present-day balance more in favour of the char and trout has been made. This experiment with populations involved the annual trapping of the perch in spring (from 1940), and the gill-netting of pike each winter since 1944–45. Up to date about 95 tons (96,500 kg.) of perch (estimated at about nine-tenths of the original population) and 10½ tons (11,00 kg.) of pike have been removed from the lake. The gill-netting of the pike has resulted in the removal of the larger individuals, fish ranging from 40 to 105 cm., the majority 60–70 cm., in length. The numbers and weight of pike caught from 1943 to 1947 showed an 'abrupt reduction' of the population (Worthington 1949), and although subsequently some rise in the catches has occurred the gill-nettings have kept the population at a low level compared with that of pre-netting days. The effect of this reduction of the pike on fish, working through the food relationships, has been considered by Worthington (1949) on the results obtained to 1947; these and other data obtained since show the effect on perch, trout and char.

Since the perch form so large a part of the food of pike the steady removal of the pike must have greatly reduced the pressure of predation on these fish. The most apparent result of this is the marked increase in the numbers of older and larger perch, since more survive now to grow older and so larger (Le Cren, personal communication). The standard seineings for fish carried out in Windermere showed that from 1941 to 1944 the average number of trout caught was 72, and from 1945 to 1952 it was 340. There has therefore been, as indicated by these nettings, an increase in the population of trout during the period when the pike were being reduced. Some corroborative evidence for this increase is supplied by the general opinion of local anglers that their catches have to some extent increased in number and average size. Predation on the char is confined to the breeding individuals, particularly those of the autumn-spawning population, since the pike crops only the sexually mature and older fish. The number of char of the autumn-spawning population on a certain breeding ground has been estimated for each year since 1939 by means of a standard gill-netting (Worthington 1949). The numbers so caught given by Worthington for 1939–47, and recorded by me for subsequent years are, 1939 (33), 1940 (25), 1941 (69), 1942, (66), 1943 (66), 1944 (82), 1945 (175), 1946 (101), 1947 (350), 1948 (236), 1949 (114), 1950 (208), 1951 (238),

1952 (176), 1953 (121). These results show that since the intensive annual winter gill-netting for pike began in 1944–45 the number of char caught has always been much greater than before this pike netting started, and it seems justifiable to associate the increase in this char population with the removal of its chief predator, the pike. Cannibalism among pike of any size appears to be rare in Windermere so that the reduction in numbers of the predator has probably had little if any effect on the survival of this prey. Since the minnow and stickleback contribute so little to the diet of the pike taken by gill-net these species will be almost unaffected by removal of predation pressure.

Two main conclusions emerge. First there seem to be in Windermere no clear signs of deliberate choice by the pike of any particular species of fish from among those present at any one time (the only suggestion of conscious selection is given by the relative numbers of minnows and sticklebacks in the food). It is rather external factors such as relative abundance and seasonal availability that determine the species of prey, even though the size of the individuals of the species eaten is selected by the pike. Secondly, the reduction of the numbers of pike seems to have demonstrated that the feeding habits of the pike have a marked effect on the survival of other fish species and so are a major factor in determining both the numbers of a species present and the structure of its population.

ACKNOWLEDGEMENTS

My thanks are due to Mr G. J. Thompson, the laboratory steward, and to Messrs T. N. Martindale, K. Shepherd and F. Prickett of the laboratory staff, who have been responsible, at different times during the past 10 years, for netting the pike and for the examination and recording of the stomach contents of many of them. I am indebted to Miss M. Hullock for much assistance in sorting of the data. I wish to thank my colleague Mr E. D. Le Cren for allowing me to use certain unpublished results from his study of the perch and also for his criticism of the manuscript.

SUMMARY

1. The food of pike in Windermere has been investigated from 3060 specimens, ranging from 1·05 to 105 cm. long collected by gill-net, seine-net and hand-net.

2. Of the small pike (20 cm. and less) those of 10·5–17·5 mm. feed entirely on Entomostraca, those of 35–200 mm. chiefly on fish, mainly perch fry of 10–60 mm, and to some extent on aquatic insect larvae and *Eurycercus lamellatus*.

3. Large pike (of 20–105 cm.) feed almost entirely on fish, perch and trout predominantly, char considerably, and stickleback and minnow to some extent; pike and eels are of no consequence.

4. Predation on fish shows seasonal fluctuations in intensity. Perch occur in the diet at all times but predominate from May to October; char are eaten only in November and December; trout are eaten to a greater extent from October to February; sticklebacks and minnows are eaten in spring and summer. Such seasonal variations are associated with the changes in habit of the food species.

5. Increase in the size of the pike is associated with increase in size of the food organisms eaten. Among pike of 1·05–20 cm. this is effected by a change in the kind of food, from Entomostraca to perch fry; among pike of 20–105 cm. there is a

change (1) of the fish species eaten, (2) of the size of individuals of a particular species. The pike selects the larger and older individuals of the perch and trout populations in the lake.

6. The 83% of small pike with food in their stomachs compared with 52% for large pike is probably associated with the difference in size of food animals eaten by them. Among large pike a decrease in the proportion of feeding fish corresponds to an increase in size of the pike. The lowest percentage of feeding fish is found about spawning time, the highest after this time.

7. Comparison of the fish eaten by the pike with those present in the lake leads to the conclusion that abundance and availability rather than selection by the pike determine the species eaten (with the possible exception of sticklebacks).

8. The feeding habits of the pike have a marked effect on the survival of fish in Windermere and so affect the numbers of the species and the structure of their populations, as demonstrated for the perch, trout and char.

REFERENCES

Allen, K. R. (1935). The food and migration of the perch (*Perca fluviatilis*) in Windermere. *J. Anim. Ecol.* **4**, 264–73.

Allen, K. R. (1938). Some observations on the biology of the trout (*Salmo trutta*) in Windermere. *J. Anim. Ecol.* **7**, 333–49.

Allen, K. R. (1939). A note on the food of pike (*Esox lucius* L.) in Windermere. *J. Anim. Ecol.* **8**, 72–5.

Balfour-Browne, F. (1906). On the early stages in the life histories of certain fresh-water fishes. *Trans. Norfolk Norw. Nat. Soc.* **8**, 478–88.

Frost, W. E. (1945). On the food relationships of fish in Windermere. *Biol. Jaarb.* Jg. XIII, pp. 216–31.

Frost, W. E. (1951). Some observations on the biology of the char, *Salvelinus willughbii* Günther, of Windermere. *Verh. int. Ver. Limnol.* **9**, 105–10.

Hunt, B. P. & Carbine, W. F. (1951). Food of young pike, *Esox lucius* L., and associated fishes in Peterson's ditches, Houghton Lake, Michigan. *Trans. Amer. Fish. Soc.* **80**, 67–83.

Larsen, K. (1951). Om geddens (*Esox lucius* L.) føde i vandløb. *Sports-Fiskeren*, **2**.

Montén, E. (1950. Studier över yngelförlusternas orsaker i fria vatten och i dammar (II). *Skr. sverig. FiskForen.* pp. 20–101.

Smyly, W. J. P. (1952). Observations on the food of the fry of perch (*Perca fluviatilis* Linn.) in Windermere. *Proc. Zool. Soc. Lond.* **122**, 407–16.

Worthington, E. B. (1949). An experiment with populations of fish in Windermere, 1939–48. *Proc. Zool. Soc. Lond.* **120**, 113–49.

Wurtz, A. (1945). Développement, biologie et nutrition des jeunes alevins de brochet (*Esox lucius*). *Bull. franç. Piscic.* **135**, 57–69.

ONCHIDORIS FUSCA (MÜLLER); A PREDATOR OF BARNACLES

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(With Plate 2)

During the summer of 1950 large numbers of the common inshore Nudibranch *Onchidoris fusca* (Müller) (= *Doris bilamellata* L.) were observed on barnacle-covered panels suspended 2 ft. below the surface from a raft moored at Millport, and reference has already been made (see Barnes & Powell 1951) to the circumstantial evidence that these dorids had been feeding on the crowded barnacles. The barnacles were mixed *Balanus crenatus* Brug. and *B. balanoides* (L.). There appears to be little factual information in the literature concerning the diet of *Onchidoris fusca* and therefore, when a similar association of these animals was seen a year later (mid-October 1951), the opportunity was taken of making more detailed observations both in the field and on submerged panels in the laboratory; these are now reported.

OBSERVATIONS OF FEEDING

Closer observations on panels brought in from the raft indicated that *O. fusca* spent long periods covering the uppermost parts of the barnacles (see Pl. 2) and, on carefully removing a number of the dorids, the opercular valves of the barnacles were seen to come away quite easily, still sticking to the anterior region of the ventral surface. There was little doubt that they were actively feeding on the barnacles. Microscopic examination of the gut contents of many such dorids failed to reveal any chitinous barnacle remains, but the oily appearance was such as could have resulted from the ingestion of the soft, yellow, ovarian material, which filled a large part of the mantle cavity of *Balanus crenatus* at this season. Further examination of the dead barnacles showed that the cirri and the remains of the chitinous exoskeleton had been left more or less *in situ*, and it seemed clear from this that the dorids were feeding only on the soft parts.

Detailed observations confirmed this. Several *Onchidoris fusca* were placed on a panel thoroughly cleaned of everything except a number of well-spaced live barnacles of various sizes, and laboratory observations made on their movement and behaviour. After making contact with a barnacle, the *Onchidoris* slowly glides up the side and eventually comes to lie over the whole or part of the opercular orifice (see Pl. 2). In the case of the smaller *O. fusca* the tendency is for the orifice to be reached at or near the rostral end; if it first comes in contact with the base of the barnacle at the carinal end it takes an upward and more or less spiral course towards the rostral end. It would seem that the steeper angle at the carinal end is responsible for this response. Once over the opercular orifice, an *Onchidoris* remains in this position for some hours, during which time the mouth and buccal parts are completely obscured by the broad veil and the mantle. It is therefore not possible to follow the feeding process visually, and the details are inevitably a matter of deduction. After feeding, the dorid moves

slowly away, often only a short distance before coming to rest, frequently alongside a barnacle, and during this rest period digestion of the ingested soft parts presumably takes place; later it begins to move more actively again.

Examination of the barnacle after the *Onchidoris* has moved away shows that the operculum, in particular the scutal valves, has been pushed down into the cavity of the barnacle, the opercular membrane being torn away from the calcareous plates in the scutal region. The method of entry is therefore quite different from that described for another common molluscan predator of barnacles, *Nucella lapillus* (L.), which, according to Moore (1938), uses the radula to force the valves apart and so reach the soft parts. In view of the impossibility of observing the details of the process in the case of *Onchidoris fusca*, it is not possible to say with certainty exactly how entry is effected. It is possible that enzymes are secreted which aid in effecting penetration, or that the narrow radula, even though much reduced in this species, and the chitinous armature of the labial cuticle (see Eliot 1910, Alder & Hancock 1845–55) may play a part, but a simpler explanation may be advanced, namely that pressure is exerted on the operculum which is eventually broken away at its attachment to the compartments. This is supported by the fact that, in general, the opercular membrane breaks away in the scutal rather than the tergal region, for it is here that a pressure exerted perpendicularly downwards will be most effective since the scutal valves tend to be flatter than the tergal valves and to lie in a more horizontal plane. Once this edge is ruptured, contraction of the mucles closing the operculum cannot be effective and access is afforded to the soft parts of the barnacle. The soft parts could then readily be removed, partly by the loosening action of the radula, but perhaps largely by the action of the *ingluvies buccalis* or buccal crop which appears to function as a suctional organ (see Eliot (1910) for further description and references), and which is present in certain dorid Nudibranchs (Onchidoridae and Goniodoridae), including *O. fusca*, which have a reduced radula.

It would seem that the feeding behaviour described above for *O. fusca* was closely conditioned by the stimuli involved in the sequence outlined, since portions of fresh barnacle ovarian material repeatedly placed in close proximity to *O. fusca* were invariably left untouched. There are few available animals in the zone inhabited by *O. fusca* with which such a series of stimuli leading to feeding could take place and it may therefore be suggested that the food of *O. fusca* may be limited to barnacles although, as Moore (1938) has pointed out, *Nucella lapillus* which also usually feeds on barnacles, as described above, can adopt an entirely different mode of feeding, namely boring through the shells of *Mytilus edulis* L. However, since as Forrest (1951) has recently emphasized, the usual diet of this suction feeding group of dorids is Ascidians and encrusting Polyzoa (he quotes *Goniodoris nodosa* (Mont.) as a typical example), it may be that these adults of *Onchidoris fusca*, which almost certainly had developed from veligers settling directly on the panels, had perforce adapted themselves to a diet of barnacles. On the other hand, comparative specificity of diet in the Nudibranchiata does not seem uncommon, ranging from *Calma glaucoides* which feeds on fish eggs and *Melibe* which captures Crustacea (Eliot 1910) to certain less specialized suction feeders. Hunt (1925) has also noted definite associations of various Aeolididae and dorids with certain hydroids, Polyzoa and sponges.

Photograph taken from above of *Onchidoris fusca* (Müller) feeding on *Balanus crenatus* Brug. of various sizes growing on a dark Bakelite panel. × 1. For description see text.

The laboratory investigations have given some information on the extent of predation by *Onchidoris fusca*. The barnacles used had grown on a panel under raft conditions and were well-grown, well-spaced individuals, from 8 to 24 mm. carino-rostral length. Forty-eight were killed and their soft parts removed by sixteen *O. fusca* of various sizes (ranging from 15 to 30 mm. length) in 11 days. The time spent by a dorid on a single barnacle ranged from 5 to 20 hr., varying a great deal with the size of both the dorid and the barnacle.

SUMMARY

The common inshore Nudibranch, *Onchidoris fusca* (Müller), has been observed feeding on barnacles, and the feeding behaviour and the extent of predation followed. The dorid effects entry by rupture and downward displacement of the operculum, and feeds only on the soft parts of the barnacle. It is probable that ingestion takes place largely by suction, involving the action of the buccal crop, the presence of which in this and certain other dorids is associated with a much reduced radula. The possibility that the diet of *O. fusca* is restricted to barnacles is considered.

REFERENCES

Alder, J. & Hancock, A. (1845–55). *A Monograph of the British Nudibranchiate Mollusca*, Parts I–VII. London: Ray Society.

Barnes, H. & Powell, H. T. (1951). The growth-rate of juvenile *Asterias rubens* L. *J. Mar. Biol. Ass. U.K.* **30**, 381–5.

Eliot, C. (1910). *A Monograph of the British Nudibranchiate Mollusca*, Part VIII (Supplementary). London: Ray Society.

Forrest, J. E. (1951). Feeding mechanisms in Dorid Nudibranchiate Mollusca. Abstract in *Programme* (p. 70). British Association Meeting at Edinburgh, August 1951.

Hunt, O. D. (1925). The food of the bottom fauna of the Plymouth fishing grounds. *J. Mar. Biol. Ass. U.K.* **13**, 560–99.

Moore, H. B. (1938). The biology of *Purpura lapillus*. Part III. Life history and relation to environmental factors. *J. Mar. Biol. Ass. U.K.* **23**, 67–74.

THE OCCURRENCE OF *MYTILICOLA INTESTINALIS* (STEUER) ON THE EAST COAST OF ENGLAND

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(With 1 Figure in the Text)

In view of the presence of the copepod parasite *Mytilicola intestinalis* (Steuer) in British Waters (Ellenby 1947; Hockley 1951; Cole 1951), and the consequent danger to the mussel fisheries around the coasts, surveys have been made with the object of discovering the distribution of the parasite. This paper is an account of observations made on the east coast which were planned for the express purpose of determining the possible damage or danger to the valuable mussel beds of the Wash and north Norfolk harbours.

In all three surveys have been made. The first in December 1949 was designed to discover whether or not *Mytilicola* had been introduced into the Wash area and whether it occurred in any quantity on the East Anglian coast. To that end samples were collected from the Wash beds (scalps) themselves, from the vicinity of King's Lynn dock, from some of the north Norfolk harbours, and from Yarmouth, Lowestoft and Felixstowe. The samples, which were of twenty-five mussels varying in length between 5·5 and 5·9 cm., were preserved in sea-water Bouin fixative and dealt with in the manner described by Cole & Savage (1951). It was found that *Mytilicola* only occurred at Felixstowe; here almost all the mussels were infected with an average number of 6·5 parasites per host. In view of this, observations were extended southward, samples being collected from the Rivers Roach and Crouch and from the Thames estuary at Leigh-on-Sea and Southend-on-Sea. In June 1950 a high mortality of mussels was reported to have occurred on the Whitstable beds, so samples were collected from that area and also from the beds in the River Medway. At these stations infection was found to be 100% (Table 1).

It seemed therefore, that the Wash fishery could be considered reasonably 'safe' for the time being as the parasites only occurred in the vicinity of, and south of, Felixstowe. However there was always the possibility that infection would spread, either from this area or from the north. Nothing was known of the distribution of either mussels or *Mytilicola* immediately north of the Wash. In 1951, therefore, a second and more detailed survey was made starting at Mablethorpe on the Lincolnshire coast. From information supplied by Mr G. Bolster (Fisheries Experiment Station, Conway), it was known that *Mytilicola* was not present at Grimsby. At Mablethorpe it was found that there was only one small isolated mussel population on the sewer outfall, which was only uncovered at low water of equinoctial spring tides; south from this point there were no mussels. The shore from Mablethorpe to Skegness consists of shifting sand and gravel with no stable substratum for the attachment of mussels. Further, any isolated groynes or piers present were so polished by the abrasive action

of the sand as to be almost devoid of sedentary organisms. Samples of mussels taken from the Wash and north Norfolk harbours were again found to be free of infection. So, too, were those from King's Lynn dock and the harbour entrance. These latter were of particular interest because if, as had been supposed, the parasite could be spread by transporting infected mussels on the hulls of coastal vessels, then it was most likely that infection would first appear in the vicinity of docks and harbours.

Mussels at Cromer and Mundesley, the most easterly points on the north Norfolk coast, were also found to be free of infection. The communities at these two stations were fairly isolated, occurring on the lifeboat slip and sewer outfall respectively. South of Mundesley the shore was found to be shifting sand and gravel similar to that between Mablethorpe and Skegness. This instability applies to the whole of the East Anglian coast-line, though towards Aldeburgh and Felixstowe in the south, there is a gradual increase in the proportion of gravel on the shore. Close examination showed

Table 1. *Infection of mussels in and around the Thames Estuary between February 1950 and October 1952*

	Station	Average length of mussels (mm.)	Average number of parasites per host	% infection
20 July 1950	Whitstable	57·8	11·8	100
8 Sept. 1952	Whitstable	57·3	8·7	100
14 Mar. 1950	R. Medway (1)	57·8	10·7	100
14 Mar. 1951	R. Medway (2)	58·1	15·5	100
6 Feb. 1950	Leigh-on-Sea (1)	56·9	1·1	60
6 Feb. 1950	Leigh-on-Sea (2)	56·8	1·6	56
6 Feb. 1950	Southend-on-Sea	58·6	1·9	92
18 July 1950	R. Crouch	51·3	10·0	100
18 July 1950	R. Roach	50·6	10·4	100

that mussels occurred at only a few localities. These were at Yarmouth, where they were present on the pier piles and round the harbour entrance, at Lowestoft, where they again appeared at the harbour entrance, at Southwold, within the harbour, and at Bawdsey on the foreshore. The Yarmouth and Lowestoft mussels were uninfected but the small isolated population on some old pier piles within Southwold harbour was found to be infected. Three mussels in a sample of twenty-five each contained one parasite. At Bawdsey there were several small communities of mussels on the foreshore at low-water mark. Infection here was 100% with an average of six parasites per host. A sample of mussels taken from Felixstowe at the same time, yielded an average of seven parasites per host.

It seemed, therefore, that the Wash mussels were unlikely to become infected by water-borne copepodid larvae because of the long stretches of barren shore between the infected and uninfected mussel communities. However, there was a substantial distance between Bawdsey and Southwold, yet the parasite had spread to the latter place. From information supplied by Mr J. G. Y. Thorpe, District Inspector of Fisheries, it seems unlikely that infection could have been spread by fishermen using parasitized mussels as bait. In addition, as Southwold has a small isolated harbour with practically no shipping other than visiting yachts, it seemed improbable that infection could have been spread that way. A further possibility that temporary communities had been established on the dragon's-teeth sea defences along that stretch of

coast was investigated. However, contractors who removed these defences are unanimous in stating that there were no mussels or indeed any other sedentary organisms, probably because of abrasive action of the sand and gravel in the water. It therefore seemed

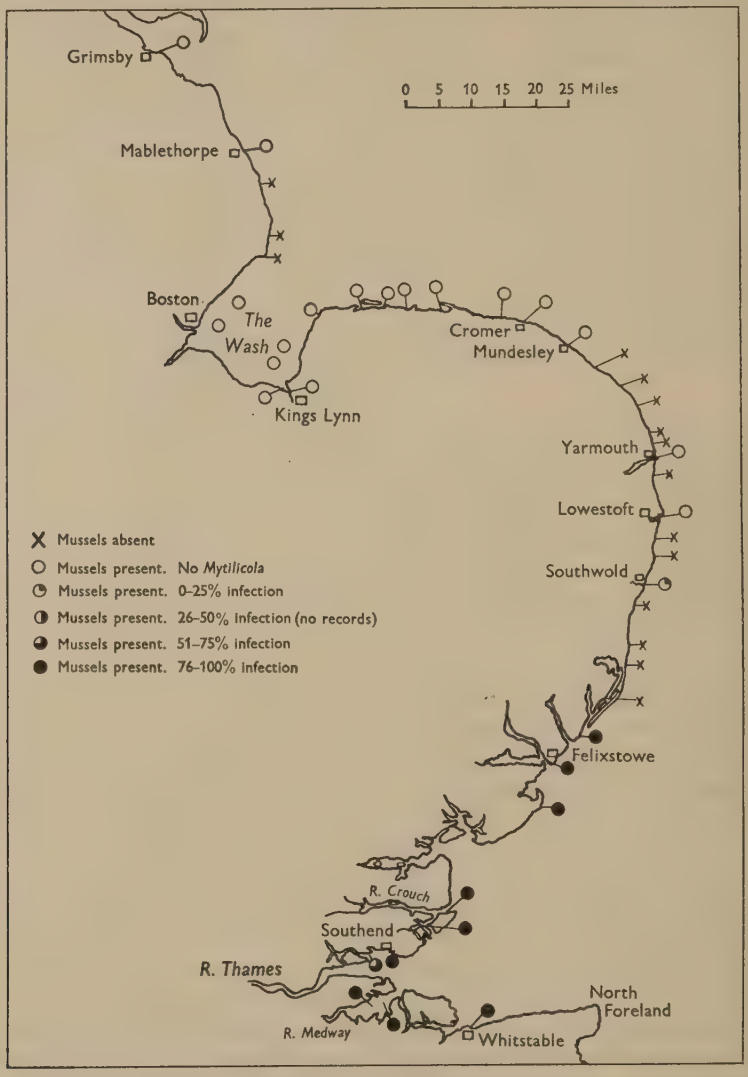

Fig. 1. Map showing stations visited during the period December 1949 to January 1953, and the distribution of mussels and *Mytilicola intestinalis* on the east coast.

impossible that the infection could have been anything other than water-borne. There are strong tidal currents in this area and though the residual water movement is from north to south it is perhaps possible that localized patches of planktonic larvae could have been carried to Southwold.

With this possibility in mind, a third survey was made in January 1953. On this occasion attention was confined to the coast between Cromer and Bawdsey though a separate sample of mussels from the harbour entrance at King's Lynn was examined and found to be free from infection. The result of this latest survey was to show that the northward spread of *Mytilicola* had not extended beyond Southwold. Of twenty-five mussels collected in 1953, only one was found to bear a single parasite (Table 2).

Table 2. *Infection of mussels at Felixstowe, Bawdsey and Southwold, and at Walton, a station closer to the Thames*

	Station	Average length of mussels (mm.)	Average number of parasites per host	% infection
19 Dec. 1949	Felixstowe	57·1	6·5	96
29 Nov. 1951	Felixstowe	55·8	7·0	100
29 Nov. 1951	Bawdsey	47·7	6·0	100
28 Nov. 1951	Southwold	50·7	0·12	12
25 Jan. 1953	Southwold	34·3	0·04	4
25 Jan. 1953	Walton	45·1	2·1	84

This sample was collected from an iron pipe alongside the old piles from which the 1951 sample was taken. As the samples were from slightly different localities and of slightly different sizes, it was not possible to decide whether the rate of infection was declining, but as there was only a maximum of one parasite per host at any time, it seemed unlikely that the parasite would multiply in Southwold harbour. The rest of the coast-line between Southwold and north Norfolk was again carefully examined to confirm that mussel communities only occurred at Yarmouth and Lowestoft. The absence of shells on the shore at other stations visited on the east coast would suggest that there are no mussels in the offshore waters. Thus the chances of water-borne parasities spreading in easy stages from one mussel bed to another up the coast are much reduced.

ACKNOWLEDGEMENTS

I would like to express my indebtedness to Mr R. Taylor, Clerk to the Eastern Sea Fisheries Joint Committee, and his officers for their kind co-operation and assistance. I would also like to thank the many east-coast fishermen who supplied me with samples and information.

REFERENCES

Cole, H. A. (1951). Le *Mytilicola* en Angleterre. *Rev. Trav. Off. Pêches Marit.* **17** (2), 59.

Cole, H. A. & Savage, R. E. (1951). The effect of the parasitic copepod *Mytilicola intestinalis* upon the condition of mussels. *J. Parasit.* **41**, 157.

Ellenby, C. (1947). A copepod parasite of the mussel new to the British fauna. *Nature, Lond.* **159**, 645–6.

Hockley, A. R. (1951). On the biology of *Mytilicola intestinalis* (Steuer). *J. Mar. Biol. Ass. U.K.* **30**, 223–32.

THE HUNGER-CYCLES OF *GLOSSINA MORSITANS* WESTWOOD AND *G. SWYNNERTONI* AUSTEN

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(With 1 Figure in the Text)

As is well known, the tsetse fly, *Glossina morsitans* Westwood, occupies in eastern Africa mainly country dominated by broad-leaved woodland of *Brachystegia* and other genera of Caesalpiniaceae, characterized by a good high canopy in the rainy season and in the dry season still with a substantial amount of shade from the leafless boughs. *Glossina swynnertoni* Austen, on the other hand, inhabits a more xerophytic zone in northern Tanganyika Territory and southern Kenya, dominated by thorny *Acacia* and *Commiphora* spp., interspersed with small thickets of *Grewia* and other plants, and affording very little overhead shade. Though some of the *Brachystegia* country has a lower rainfall than some of the thornbush, the latter has generally the lower rainfall and certainly it has a very arid aspect in the leafless season. We had therefore always supposed that *swynnertoni* was a species adapted to withstand more arid conditions. However, when both species were subjected to identical conditions of temperature and humidity (25° C. and 50% R.H.) for 24 hr., freshly emerged, unfed males of *morsitans* actually showed a greater resistance to desiccation than did those of *swynnertoni*, which lost the same, or slightly more, weight than *morsitans*, and lost a significantly higher proportion of their initial weight, which is only about 90% that of *morsitans*. Judging by these unfed flies, therefore, *swynnertoni* is by no means specially adapted to withstand desiccation (Jackson 1945).

A second line of evidence was that *swynnertoni* contains proportionately less fat and more non-fatty solids than does *morsitans*, and this suggested that it might synthesize less food reserves from the blood meal but might feed more frequently, since part of the non-fatty solids would presumably be undigested blood. This suggestion received some support from the fact that the thornbush habitat of *swynnertoni* is far better stocked with large game animals than is most of the *Brachystegia* country which harbours *G. morsitans*.

It was therefore decided to attempt to determine the hunger cycles of the two species directly. It was known that during the middle part of the dry season in September the climates of Shinyanga (habitat of *swynnertoni*) and Kakoma (habitat of *morsitans*) were very similar, while rain at this time is unlikely and would therefore probably not produce differential changes in the two places which are 200 miles apart. Kakoma (Jackson 1937) is a typical habitat of *morsitans* and seemed perfectly suitable in every way.

The experiments were performed in 1948 and 1951. In the first year the *morsitans* observations at Kakoma lasted from 12 to 27 September and the *swynnertoni* observations at Shinyanga from 12 September to 5 October, being continued a little longer in

an endeavour to make up for the low numbers of *swynnertoni* at that time. In 1951 the *morsitans* and the *swynnertoni* observations were both made from 12 to 29 September. Flies were weighed in the field on a torsion balance for 70 mg., and weights were recorded to the nearest milligram only (see Table 4, Appendix). The weight was either marked on the fly (Jackson 1937) or recorded in a book against a number marked on the fly (Jackson 1953). The weighings were done from 9 to 11 hr. and from 16 to 18 hr., East African standard time, and at all these hours readings were taken with a whirling psychrometer (Table 1), which unfortunately lacked a wet bulb in the 1948 experiment at Kakoma. The flies were caught by usually three or four catchers and brought alive in the nets, a few at a time, for weighing, marking and release. The figures in Table 1 show that at the same temperature the general climate of the habitat of *swynnertoni* is somewhat drier, as the arid appearance of Shinyanga at this season would suggest.

Table 1. *Psychrometer readings at Kakoma and Shinyanga, 1948 and 1951*

	Temperature (° C.)				Saturation deficit (mb)			
	Kakoma		Shinyanga		Kakoma		Shinyanga	
Time	1948	1951	1948	1951	1948	1951	1948	1951
0900	25·1	23·9	24·7	23·9	.	13·5	15·5	15·0
1100	28·5	27·7	28·4	29·5	.	19·5	23·5	26·1
1600	31·8	32·4	32·6	31·6	.	31·4	35·7	32·7
1800	29·9	31·0	29·8	30·1	.	28·6	29·2	29·9
Mean	28·8	28·7	28·9	28·8	.	23·3	26·0	25·9

The mean initial weight of *morsitans* (non-teneral males) destined to be recaptured was 30·0 mg. in 1948 and 29·8 mg. in 1951; that of *swynnertoni* was 25·4 mg. in both years, or about 85% of the weight of *morsitans*. Larger numbers of *morsitans* were marked, and substantially larger numbers were recaptured but the recaptures of flies at half a day's interval from release are fewer for *morsitans* because in 1948 there was a difference in method, no recaptures being made at Kakoma from morning to evening of the same day.

Sir Ronald Fisher suggested to me that the variance in weight difference classified by length of interval would give a clue to the length of the hunger cycle, the maximum variance indicating the half-cycle period and the minimum variance the whole cycle. This approach has proved very successful. The sum of squares of differences from initial weight was calculated for each interval between release and recapture, and the mean squares were found by dividing by the number of flies contributing. The differences of the variances for successive intervals were then tested for significance, with the following result. For *morsitans* there were significant rises in variance (Fig. 1) from day 0 (zero variance) to day $\frac{1}{2}$ and from day $\frac{1}{2}$ to day 1, then a fall from day $1\frac{1}{2}$ to day $2\frac{1}{2}$. The peak variance could therefore fall on day 1, day $1\frac{1}{2}$ or day 2, indicating a half-cycle of 1–2 days and a full hunger cycle of 2–4. But there is also a significant fall from day $2\frac{1}{2}$ to day 3 and then a significant rise from day 3 to day $4\frac{1}{2}$, which means that the minimum variance must occur on day 3, $3\frac{1}{2}$ or 4, which agrees with and narrows down the conclusion drawn from the half-cycle: the hunger cycle of *morsitans* is therefore something between 3 and 4 days.

For *swynnertoni*, there are significant rises in variance from day 0 to day $\frac{1}{2}$ and from day $\frac{1}{2}$ to day 1, and a significant fall from day 1 to day 2. The maximum variance could therefore occur on day 1 or $1\frac{1}{2}$, indicating a whole cycle of 2–3 days. But there is also a significant fall from day 2 to day 3 and a significant rise in variance from day 3 to day 4, which means that the minimum variance must fall on day $2\frac{1}{2}$, 3 or $3\frac{1}{2}$, of which the last is ruled out by the evidence of the half-cycle period. The hunger cycle of *swynnertoni* must therefore occupy $2\frac{1}{2}$ or 3 days. The cycle for *swynnertoni* does therefore work out shorter than for *morsitans*, but as the results stand they offer no information as to the significance of this difference, and both cycles might in fact on this evidence be just 3 days.

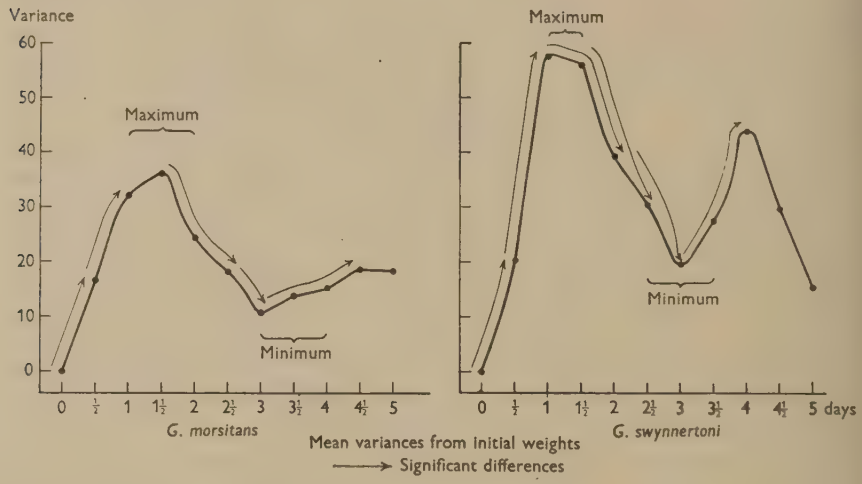

Fig. 1

However, there is other evidence of a significant difference. Omitting day $\frac{1}{2}$, because of the difference of method in this respect between the two species, we find, for days 1–$2\frac{1}{2}$, the mean departures from initial weight given in Table 2. After day $2\frac{1}{2}$ the differences between the species become insignificant, but this table is enough to show that *swynnertoni* feeds sooner than *morsitans* after the meal and therefore must have a shorter hunger-cycle.

Table 2. *Mean departures from initial weight at days 1 to* $2\frac{1}{2}$

Day	Mean departure *morsitans*	Mean departure *swynnertoni*	Difference	S.E.	Diff./S.E.
1	−3·67	+1·06	−4·73	1·033	−4·58
$1\frac{1}{2}$	−1·64	+4·09	−5·73	1·277	−4·49
2	+2·19	+4·37	−2·18	0·892	−2·44
$2\frac{1}{2}$	+1·31	+3·04	−1·73	0·837	−2·07

That the values of 3–4 days for the *morsitans* cycle and $2\frac{1}{2}$–3 days for the *swynnertoni* cycle in September are quite plausible is shown by the records of flies recaptured within 1 mg. of their initial weight, having passed through a complete hunger-cycle (Table 3).

The hunger-cycle is probably shortest in September or October; it is probably twice as long at the end of the rains.

Table 3. *Flies recaptured within 1 mg. of their initial weight*

Day ...	1	1½	2	2½	3	3½	4	4½	5	5½	6
morsitans	0	5	10	30	33	20	26	19	16	12	9
swynnertoni	3	3	8	13	8	6	3	9	2	5	5

ACKNOWLEDGEMENTS

These experiments were carried out by Mr D. L. Johns at Shinyanga in 1948 and at Kakoma in 1951, by Mr J. M. B. Harley at Shinyanga in 1951 and by myself at Kakoma in 1948. I am indebted to Dr J. P. Glasgow for co-operation in working out the data, and especially to Sir Ronald Fisher who suggested the method of determining the hunger-cycle by finding the periods of maximum and minimum variance from initial weight.

SUMMARY

1. The hunger-cycle of *Glossina morsitans* in the mid-dry season in Tanganyika is between 3 and 4 days and for *G. swynnertoni* it is 2½ or 3 days.

2. This explains why it is that *G. swynnertoni*, which from laboratory evidence is not more resistant to desiccation, is able to live in a more arid environment than *G. morsitans*, in association with a generally higher density of host animals.

3. It is supposed that *G. morsitans* on the contrary is not adapted to frequent feeding, but to synthesizing more food reserves from each meal, and that it can only function normally in a well-shaded environment.

REFERENCES

Jackson, C. H. N. (1937). Some new methods in the study of *Glossina morsitans*. *Proc. Zool. Soc. Lond.* 1936, pp. 811–96.

Jackson, C. H. N. (1945). Comparative studies of the habitat requirements of tsetse fly species. *J. Anim. Ecol.* **14**, 46–51.

Jackson, C. H. N. (1953). A mixed population of *Glossina morsitans* and *G. swynnertoni*. *J. Anim. Ecol.* **22**, 78–86.

APPENDIX

Table 4. *Gains and losses at ½-day intervals (mg.)*

	G. morsitans										*G. swynnertoni*									
Day	½	1	1½	2	2½	3	3½	4	4½	5	½	1	1½	2	2½	3	3½	4	4½	5
+22	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
+21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+18	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
+17	1	.	.	.	.	.	.	.	1	.	2	1	2	.	.	.	.	.	.	.
+16	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
+15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+14	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.
+13	.	.	.	1	.	.	.	1	.	.	.	3	.	.	1	.	1	1	.	.
+12	.	1	.	.	.	.	.	.	.	.	1	.	.	2	1	.	1	.	.	.
+11	.	.	.	.	.	.	.	.	.	.	1	2	1	2	.	.	.	.	1	.
+10	.	.	2	2	1	.	.	.	.	1	3	4	1	5	1	.	1	.	.	.
+9	.	2	.	1	.	1	1	.	1	.	3	2	4	.	4	.	1	.	2	.
+8	.	.	.	2	3	.	.	.	.	1	4	2	3	1	3	2	1	1	.	.
+7	1	2	1	1	3	3	2	.	3	1	2	1	3	3	1	1	.	.	.	.
+6	.	1	3	1	5	.	6	3	1	3	4	7	3	5	1	2	.	3	1	.
+5	1	.	1	5	4	5	3	4	3	2	2	2	3	6	5	.	1	1	.	.
+4	1	2	1	9	6	3	4	.	3	.	.	1	5	7	6	1	3	.	.	.
+3	1	1	7	8	6	6	4	3	6	4	3	.	2	.	1	.	2	.	.	.
+2	1	1	1	8	8	12	12	3	7	4	6	.	4	3	1	2	.	.	.	2
+1	1	.	3	6	13	11	5	7	8	6	2	1	1	3	4	4	2	2	1	.
0	.	.	1	2	7	13	9	12	5	5	5	1	2	3	4	2	1	1	4	1
−1	4	.	1	2	10	9	6	7	6	5	13	1	.	2	5	2	3	.	4	1
−2	19	.	.	1	3	5	7	2	5	1	45	2	1	1	4	1	2	2	.	.
−3	44	10	2	1	3	4	6	6	8	2	51	6	.	.	1	1	3	1	2	1
−4	45	14	3	.	1	1	2	4	3	7	42	12	2	1	1	.	1	.	2	2
−5	8	18	4	3	.	2	4	3	7	2	20	5	3	1	.	3	1	2	1	1
−6	8	12	2	1	1	1	2	.	1	3	9	7	3	.	.	1	.	.	.	.
−7	1	7	5	1	.	2	.	1	1	1	7	4	.	.	.	1	.	.	.	.
−8	2	3	3	.	2	1	.	.	1	.	3	2	.	1	.	.	.	.	.	1
−9	.	1	.	2	1	.	.	.	1	.	1	.	.	.	1	.	.	.	.	.
−10	.	.	2	.	.	.	1	.	.	.	.	1	.	.	.	.	.	1	.	.
−11	.	.	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
−12	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
−13	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	1	.
−14	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
−15	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.

A NEW TYPE OF ELECTRICAL FISH-CATCHER

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(With 1 Figure in the Text)

Since the equipment was required for fish population studies in hill rivers and streams where access is difficult and the fish small, it had to be quite portable and capable of catching fish down to 1 in. (2.54 cm.) in length. It has been used since November 1953 and proved satisfactory. Information available suggested that pulsed direct current was likely to be the most effective way of using the power available. It was therefore decided to try using a saw-tooth power oscillator. Burnet (1952) suggests a possible circuit, but gives no circuit constants.

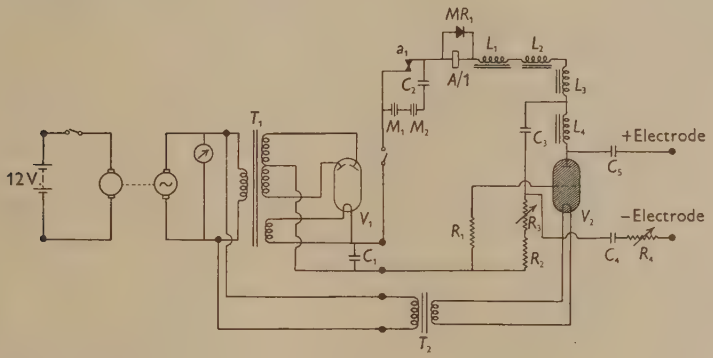

Fig. 1. Circuit of electrical fish catcher:

R_1, 100,000 Ω, ½ W.
R_2, 500 Ω, w/w, 20 W.
R_3, 500 Ω, w/w, potentiometer 25 W.
R_4, 1850 Ω, w/w, potentiometer 25 W.
C_1, C_4, 8 μF. 100 V. d.c.
C_2 0·5 μF. 1000 V. d.c.
C_3, 2 μF. 2000 V. d.c.
C_5, 4 μF. 1500 V. d.c.
L_1, 20 H.
L_2, L_4, 15 H.
L_3, 25 H.
V_1, CV 31 (U 20)
V_2, CV 1144 (NGT 5)
T_1, pri. 0–230 V.
sec. 500–0–500 V., 200 mA. 4 V. 3 A.
T_2, pri. 0–230 V.
sec. 2 V. 5 A.
$A/1$ relay 170 Ω
MR_1, 280 LU, 804 A.
M_1, M_2, metrosil unit taken from ex-R.A.F. wing de-icer Ref. no. 5U/516.

The power supply for the present apparatus is a 12 V. 40 A.H. accumulator driving a rotary convertor, giving an output of 230 V. a.c. 100 V.A. This supply feeds a high voltage transformer and rectifier circuit supplying 750 V. d.c. at 0·15 A. The free running saw-tooth oscillator (Fig. 1) consists of a mercury-vapour thyratron (NGT 5), with an inductive and capacitive network producing approximately 20 pulses/sec. At this pulsing rate, the pulse lasts for 10 msec. with a space of 40 msec. The peak voltage appearing across the electrodes, when immersed in water, is approximately 500 V., and rises to 1100 V. when the electrodes are an open-circuit. A small amount of

tuning can be carried out by the 500 Ω rheostat R_3. This is considered necessary because of the variations in thyratrons, a violent 'thudding' being noticed if the circuit is out of tune. The 1850 Ω rheostat R_4 is used as a power output control, varying the output between full and quarter power. It was found, while using the catcher in the field, that the intermittent removal of the electrodes from the water produced a condition in which the thyratron conducted continuously, switching off the h.t. being the only cure. To prevent this occurring the relay A/1 and metal rectifier were incorporated in the h.t.+ line. The function of this circuit is that the metal rectifier produces a voltage in opposition to the h.t. voltage while the thyratron is pulsing, but when the thyratron fires continuously, this opposing voltage no longer exists, and the relay operates breaking the h.t. line. With the removal of the h.t. the circuit automatically resets and pulsing begins again. Since no time-delay switch is fitted it is necessary to let the thyratron filament warm up for at least 1 min. before switching on the h.t. It is essential that this valve be mounted in a vertical position with the anode at the top.

For stream work the positive electrode consists of a sheet of perforated half-hard 16 s.w.g. aluminium 9 × 11 in. fastened to a waxed wooden pole. The negative electrode is a piece of ½ in. mesh wire-netting 18 × 36 in. Each electrode is connected to 33 yd. of single-core flexible high-voltage cable. In use the negative electrode is placed on the river-bed just down stream from the stop-net, and the positive electrode is worked downstream towards the stop-net. If the stream is fairly wide, two positive electrodes are used, so as to give better stopping and fishing coverage. For use in fishing along a lake shore for small fish hidden under stones, two metal-framed pond-nets, with the output cables connected to the frames, have proved satisfactory. This gives a more concentrated field between the electrodes, since two operators with a net electrode each can work along the shallows together about 6–8 ft. apart. When fish are disturbed by the electrical field they swim towards the surface and are easily scooped up in the net. The equipment is in four main sections: d.c./a.c. converter (type no. 1, ex-army), 60·5 lb. (30 kg.); rectifier unit, 20·5 lb. (10 kg.); oscillator, 31·5 lb. (15·4 kg.); 12 V. 40 A.H. accumulator, 49·5 lb. (24 kg.).

Table 1. *Effects of fish catcher on brown trout in a concrete tank 28 × 3 ft. containing 2 ft. of water*

Mean length of fish (cm.)	Power control setting	Effect
15	Low	Stunned with electrodes 14 ft. apart
	Full	Stunned with electrodes 28 ft. apart
10	Low	No apparent effect
	Half	Agitated between 28 ft. and 14 ft. but stunned if close to electrodes
	Full	Stunned with electrodes 20 ft. apart
7 (year old)	Low	No apparent effect even when electrodes brought within 2 ft. of each other
	Full	Stunned when electrodes 10 ft. apart

Tests were carried out in a concrete tank 28 × 3 ft., the water being 2 ft. deep, using brown trout (Table 1). Both electrodes were of the perforated aluminium sheet type attached to wooden poles. The electrodes were held so as not to touch the bottom

or sides of the tank. The same electrodes were placed diagonally in a tank 14 × 14 × 3 ft. deep keeping them clear of the sides and bottom. This tank contained fish of a mean length of 20 cm. With the power control set to the 'Full' position the fish were very agitated and became stunned within a 4ft. radius of either electrode, the fish swimming towards the surface before losing control and sinking to the bottom.

Table 2. *Brown Trout caught in two stretches of Rydal Beck*

First fishing	Second fishing	Length (cm.) Largest	Shortest
36	9	20·7	6·1
40	15	19·0	5·5

(One frog was also caught.)

Trial fishings done in the head-waters of Rydal Beck, a typical hill river, and the River Bela, a lowland type, gave the results set out in Tables 2 and 3. The total ion concentration in the water of the Rydal Beck is 0·465 mequiv./l, and of the River Bela 3·025 mequiv./l. The tests in the River Bela were to find out if the catcher would prove effective in hard waters. Rydal Beck is approximately 20 ft. wide, and the depth varied between 3 in. and 2 ft. 6 in.; the bottom consists of solid rock and large stones.

Table 3. *Results of four fishings on different stretches of the River Bela*

	Number caught	Length (cm.) Largest	Shortest
Brown trout	85	29·0	6·5
Minnows	29	8·0	2·0
Sticklebacks	16	4·7	3·2
Eels	14	35·0	12·0
River lamprey	3	16·0	13·0
Bullheads	46	9·3	3·7
Crayfish	1	11·5	—
Frog	1	—	—

The River Bela, at the point fished, is approximately 50 ft. wide, and the depth varied between 6 in. and 2 ft. 6 in.; the bottom consists of small stones and sand compacted into a level surface with *Ranunculus* clumps. A point of interest, noted while working on the River Bela, was that when the electrode was held about 4–6 in. from the bottom, the bottom fauna was agitated, *Ecdyonurus* nymphs coming out from between the stones and sitting on the top of them.

ACKNOWLEDGEMENTS

My thanks are due to the Director of the Freshwater Biological Association for his criticism and help with the paper, and to Mr D. R. Swift for help in the testing of the apparatus in the field.

REFERENCE

Burnet, A. M. R. (1952). Studies on the ecology of the New Zealand freshwater eels. I. The design and use of an electric fishing machine. *Aust. J. Mar. Freshw. Res.* **3**, 111–25.

AN INEXPENSIVE MULTIPOINT RECORDER FOR FIELD USE

By D. A. KEMPSON and A. MACFADYEN

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(With 3 Figures in the Text)

In many biological researches the need is felt for a simple multi-point recorder which is independent of mains supplies. In the present instance it was necessary to record temperature to an accuracy of 0·25° C. in about ten sites once an hour for a week in connexion with an investigation of microclimates. It was not necessary that the equipment should be particularly compact or portable, but the measuring probes themselves had to be small enough to fit in the spaces in soil or vegetation where insects and other small invertebrates live. As far as we are aware, commercially available equipment fails to meet this specification and is prohibitively expensive. Although no new physical principles are introduced in this apparatus we have been stimulated by the interest already shown in microclimate equipment by workers in a great variety of fields, to give a description of the device if only to show that it can be made in a normal small workshop and to indicate the few practical difficulties which we encountered. It should be stressed that, although used in this instance with thermistors as probes for reading temperatures, the recorder itself could equally well be used to record humidity, light intensity or any other physical quantity which can be made to deflect a meter needle. The apparatus was constructed almost entirely from government surplus parts; if a more portable version were required this could easily be made at greater expense. The cost of the prototype was under £20 (£6 being for 'thermistors' and £6 for the clock) and about 100 man-hours for construction.

The basic principle of the recorder unit is to photograph on 35 mm. film the silhouette image of a meter needle passing over a narrow slit. The record appears as a thin line with a break indicating the needle position. The film is wound and the meter is switched to a new measuring element by a solenoid-operated gear train, and the solenoid in turn is supplied via relays through a clock whose hand closes a small switch as many times per hour as there are measuring circuits. A delay circuit consisting of two relays, one of which is slugged and has a large condenser in parallel, is used to control all switching operations. One relay is closed for the same time as the clock hand makes contact, this delay period being used to allow the meter needle to come to rest before the exposure is made. The other relay closes and opens about 3 sec. later than the first; this period is used to control exposure time. Between each sequence no current flows in any circuit.

Battery consumption is reduced to a minimum and is almost the shelf life of the four separate batteries whose functions and voltages are:

(1) Meter circuit battery—Ever Ready 1·5 V. 'all dry' AD 4. This must remain constant within 1% and is first run down through a 30 Ω resistance for 3 days to

1·45 V. at which voltage there is a relative 'plateau' in the discharge curve. The battery then maintains this voltage for many weeks because the drain is only about 0·5 mA. for 84 sec. in each hour.

(2) Solenoid battery—9 V. discharged at 50 mA. for 36 sec./hr.

(3) Relay battery—22·5 V., 16 mA. for 84 sec./hr.

(4) Lamp battery—4·5 V. discharged at 200 mA. for 36 sec./hr.

The last three are made up from the requisite number of Ever Ready 126 batteries in series.

In order that the apparatus may be operated by semi-skilled operators it is essential that any faults should be apparent at once when the weekly film-changing visit is made. A test meter with a selector switch and appropriate shunts is therefore built in; the current in the return lead of all four battery circuits is thus made to give the same deflexion and a departure from this reading indicates a circuit fault or a low battery. A press button in parallel with the clock allows the operator to work the apparatus and thus check its operation and also the resistance of the thermistors, whose long leads are a potential site of damage.

The 60—0—60 μA., 250 Ω meter is connected in a simple Wheatstone bridge circuit with a preset variable ratio arm for adjustment of the relation between the mean temperature and the mid-scale reading and a preset variable shunt across the meter to adjust the range expansion. The apparatus could be made considerably more sensitive at the expense of range or the range could be increased at the expense of sensitivity.

To work the thermistor selector switch and film feed a solenoid-operated pawl gathers at each impulse from the clock switch one tooth of a ratchet with as many teeth as there are poles in the selector switch. The pawl must be self-locking to overcome the backlash caused by film tension. Since normal 'Uniselector' switches require considerable power for operation, a special low friction switch was made with silver-tipped wiper arms making contact with silver studs.

At the opposite end of the spindle to the selector switch is coupled an 8 to 1 reduction gear terminating in a spindle turning the core of a 35 mm. miniature film cassette. This spindle must be long enough to carry a sliding extension piece, with a locking screw and a slotted end to engage in the internal cross-bar of the cassette core. The engagement of the core must be quite loose, to allow for any slight misalignment during rotation.

The film magazine is a rectangular box (Fig. 1) with an internal partition forming two chambers of unequal size. The larger one holds 100 ft. of 35 mm. positive film which feeds through a velvet light trap in the partition close to the roof, into a cassette in the smaller chamber. The cassette is held with its light trap in close alignment with the partition trap, and access for changing it made through a light proof hinged door, L-shaped in section and forming the top corner edge of the box. Access to the fresh film spool is through one side of the box made as a lid, held by a nut on a bolt running across inside the box and supporting the film through the centre of the spool. The film feeding off from the fresh spool is made to pass close to the roof by a velvet-lined platform about 40 mm. long, leading it into the partition trap. Above the platform and transversely to the film, an opening about 3 by 30 mm. is cut in the roof, over which are fixed two thin metal plates to form a slit 0·1 mm. wide through which light

can pass to the film inside. These plates must be electrically earthed to prevent electrostatic charges influencing the pointer and held by spring washers at one end to allow for differential expansion. The box was of black Perspex in the original. The meter registering the bridge current is attached to the top of the box, face down with the centre position of the needle at right angles to the slit and about 0·5 mm. away from it. A very small nick is made in one of the slit edges immediately below one side of the meter needle at the zero position, and another near one end to act as location points in the slit image formed on the film when reading the records against a scale. The distance from the slit to the film is 4 mm. and the resulting image on the film is very little wider than the width of the slit gap. As positive film is normally supplied wound emulsion in, the slit exposure is made through the base of the film, which simplifies the design and keeps the winding load on the solenoid unit to the minimum.

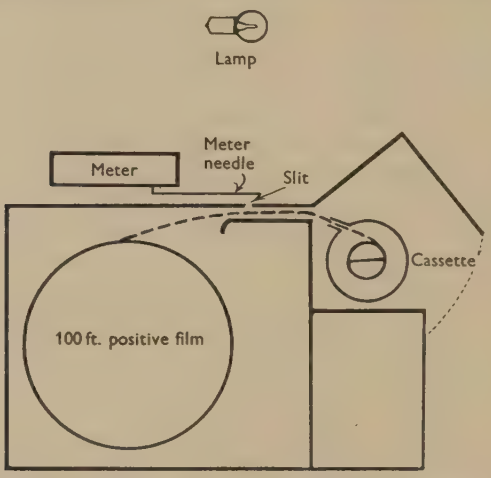

Fig. 1. Diagrammatic section through the film magazine.

The light source for exposing the film is a 6 V. 0·3 A. torch bulb placed at a distance of about 130 mm. from the slit, orientated so that the smallest overall size of the filament is presented at right angles to the centre of the slit. The position of the light source must not be moved once the recorder has been calibrated. Exposure is adjusted by means of a variable resistance in series with the bulb. To complete the unit, a light-tight removable cover completely encloses the bulb, meter and slit. The spacing between individual slit images on the film with the switch points and gearing described was quite consistent throughout a 7-day run at about 0·6 mm. The film apparently keeps to the walls of the take-up cassette and the expected slow increase in spacing as the core diameter enlarges does not occur. The space between records (Fig. 2) may appear generous in comparison with the image size, but a safety margin is advisable to prevent congestion on the rare occasions when slight bunching occurs. As an example one 8-day record consisted of 2304 slit images and occupied a length of film 130 cm. long. Longer runs than 7 days are not advised, however, owing to the risk of the recorder stopping due to film winding stresses overloading the solenoid.

The simple method of using a clock hand to make contact with studs is not suitable for this type of recorder without some modification. The slow make and break sometimes produces more than one closed circuit, which upsets the synchronization and makes interpretation of the records very difficult. These objections were entirely

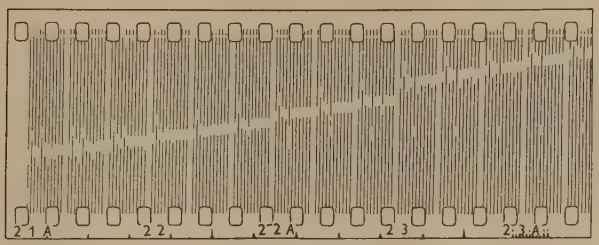

Fig. 2. A portion of a record approximately actual size.

eliminated by the incorporation in the wiper arm of a simple snap action switch (Fig. 3). The minute hand is prolonged in the form of a springy phosphor-bronze bow with a silver shoe so mounted at its tip as to make a slight angle with the arc of movement of the hand. On the leading face of the shoe is cemented by means of shellac a thin piece of paxolin covered with a silver strip, so that only the distal tip of the original shoe is exposed.

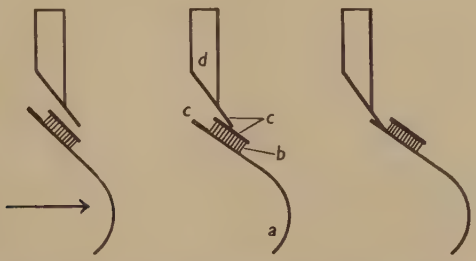

Fig. 3. Diagram showing the snap action of the clock switch. *a*, Phosphor bronze bow attached to clock hand; *b*, paxolin; *cc*, silver strip; *d*, fixed stud.

When the outer (insulated) silver strip wipes against the knife edge of a stud, it cleans the surface of the latter and bends the phosphor-bronze bow until the trailing edge is reached. The conducting shoe is then thrown against the stud by the recoil of the spring and a definite snap contact results. The knife edges of the studs consist of sheet silver and are protected by a condenser connected across them.

Reading of the film is done by means of a film-strip projector and a calibrated screen, zero points being provided by the nicks in the slit image and a dimmed standard reading at every twelfth exposure, when a fixed resistance replaces the thermistor. Photographic enlargements on document paper have also been used for records which are subject to intensive study.

When thermistors are used in a device of this sort calibration is normally complicated because the characteristics of the individual thermistors vary; however, by selection of thermistors whose characteristics were already similar and by the use of series and parallel resistances to increase the (hot) low resistance end of the working range and decrease the (cold) high resistance end it was found possible to fit all characteristics to a single standard; thus a given meter position corresponds directly to a definite temperature.

NOTE ADDED IN PROOF

Since this paper was written an important paper has been published by Mortimer & Moore (1953). Among other valuable features this paper gives many references, an improved method of calculating Wheatstone bridge parameters, information on ageing of thermistors, and details of an improved dry battery for constant voltage work.

REFERENCE

Mortimer, C. H. & Moore, W. H. (1953). The use of thermistors for the measurement of lake temperatures. *Mitt. int. Ver. Limnol.* **2**, 1–42.

LETTER TO THE EDITOR

The Editor,

The Journal of Animal Ecology

Dear Sir,

In the previous number of this *Journal*, G. R. Williams (1954, p. 17) states that I have claimed a 4-year cycle in the Greenland ptarmigan *Lagopus mutus*, which the evidence does not justify. He is presumably referring to a footnote in Lack (1951, p. 422, Table 5) in which I was careful to omit all mention of cycles and spoke of 'apparent peaks' and 'average apparently 4·4 years but very erratic'. My implicit conclusion was that the fluctuations were irregular.

May I take this opportunity to plead that the term 'cycle' (as applied to populations) should be restricted to those cases in which the interval between successive peaks is approximately equal? This holds in the lynx (*Lynx canadensis*) and by implication in the other carnivores, the rodents and gallinaceous birds of the 10-year cycle, and it may also hold in the animals affected by the 4-year cycle of lemmings. The evidence is inconclusive, as yet, as regards voles. In British gallinaceous birds, including the red grouse (*Lagopus scoticus*), Moran (1954*a*, *b*) has found no real evidence for an oscillatory or cyclic tendency.

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25 *May* 1954

REFERENCES

Lack, D. (1951). Population ecology in birds. A review. *Proc.* 10*th Int. Orn. Congr.* pp. 409–48.

Moran, P. A. P. (1954*a*). The logic of the mathematical theory of animal populations. *J. Wildl. Manag.* **18**, 60–6.

Moran, P. A. P. (1954*b*). The statistical analysis of game-bird records. II. *J. Anim. Ecol.* **23**, 35–7.

Williams, G. R. (1954). Population fluctuations in some Northern Hemisphere game birds (Tetraonidae). *J. Anim. Ecol.* **23**, 1–34.

REVIEWS

AN ECOLOGICAL TEXT BOOK

Eugene P. Odum (1953). *Fundamentals of Ecology.* Pp. xii + 384, 119 text-figures. Philadelphia and London: W. B. Saunders Company Ltd. Price 32*s.* 6*d.*

All ecologists must have felt how much they need a fairly short general text-book that deals with the subject in an up-to-date way and, above all, discusses ecological processes and balance, not just habitats, distribution, statistical dispersion and completed adaptations to existence. This need is felt in particular by graduates launching into their first solid research, after university courses in zoology that, at any rate in this country, give the student little idea of process in nature or of the difficulties of measuring it. Prof. Odum's book has great attractions. It is not too long or expensive, cites plenty of recent research on live topics, successfully deals with population ecology, and is written in a lively and even provocative style and illustrated with very carefully chosen examples.

However, some general reservations need to be made. The book is not really about general ecology: rather it is about the ecology of animal populations and communities set against an informative context of plant ecology and physical features. To this extent the title is misleading, for one will not, indeed could not within this compass, expect to find much about the fundamentals of plant ecology. Otherwise, the book has a refreshingly broad outlook. The author's own special research has been upon the ecology of bird populations, partly on their relations to vegetation, and this has ensured a real appreciation of the field natural history side of ecological research. His brother H. T. Odum has contributed useful material in the parts about the circulation of matter and energy in ecosystems, and upon human ecology.

A second reservation applies perhaps more to all text-books on animal ecology than to this particular one. It really concerns all 'authoritative' books on anything. It is the absolute necessity for students to read them as critically as they would read a special paper or monograph. Animal ecology is still in such an embryonic stage of thought (though it has all too many facts and theories to swim about in), that it can hardly be said yet even to have completed its neural fold. Its facts are still rather chaotic, many of them not facts at all; its theories are poised uneasily between complete arm-chair pipe-dreams (valuable as models for thought) and ready-to-wear mathematical models that fit badly and are already bursting at the seams. And we have still not solved satisfactorily our chief dilemma—how to study the full complexity of interlocking natural communities without sacrificing depth to breadth of research.

Prof. Odum has picked a sane path among these difficulties. He divides his book into three parts: 'Basic ecological principles and concepts', 'The habitat approach', and 'Applied ecology'. One might wish to quarrel with the vague language of such titles, which seems to be an endemic disease of American ecology (what is the difference between a principle and a concept? a habitat approach seems to mean an oecological approach?), but the system is sound. It insists that there are universal principles of population structure and dynamics, and of community organization, applying to all kinds of places in the world. Once equipped with them, and with a certain amount of special technological training suitable to the peculiar situation studied, a research worker ought to be able to tackle equally well the ecosystem of a meadow, a river or the seashore. Provided of course that he is interested in it. In the past he has often had superb technological skill with a group (say fish or scale-insects) or a habitat (say an estuary or dying pine trees), without benefit of these general principles. Dr Johnson said somewhere that a man may be sincere in good principles, without having good practice; but ecology has usually worked the other way round. This has led to the development of separate disciplines, especially in applied biology. A book like Odum's encourages one to think that these divisions may to some extent be breaking down, and that in future we may see the lion lying down with the lamb, the whale with the scale-insect, and the sea-lamprey with the lemming.

Having isolated what seem to be general principles applicable to any ecosystem containing animals, the author then treats of habitats separately. The first part of the book is the really stimulating one, the others being on more or less conventional lines, and the third really too

condensed to serve a useful purpose, since it occupies only 10% of the whole text. It is presumably put in to catch the numerous eyes of applied ecologists. I would have thought they could find in other directions much fuller information about the use and abuse of natural resources, soil erosion, wild-life management and the future of human population. However, the concluding sentence might have been printed in very large poster block capitals by itself: 'Consequently, a lot of diligent study of man and nature (as a unit, not separately) is in order before we can even begin to entertain the idea that we are masters of our destiny.'

I have emphasized the readable and interesting form of this book. It does not suffer from chattiness, indeed still has a certain stiffness in some of the joints, as in the unnecessarily formalistic arrangement within the chapters of Part 1, into Statement, Explanation and Example. This system is however redeemed by the great trouble that has been taken to find cogent and often new examples; and by the really excellent figures, mostly redrawn by Mrs Odum. There are 119 illustrations which include a good many photographs as well. The printing of the text is first-class, though the book is rather weighty, not only with ideas but with the china-clay necessary for printing photographs on the ordinary page.

Part 1 is arranged as follows: Ch. 1 is a general introduction on conventional lines. Ch. 2 comprises the ecosystem and cycles of matter, with a note on the idea of 'niche'. The author does not make it clear that Grinnell's concept of niche was quite different from mine, in emphasizing the distributional and spatial position of a species, whereas I used the notion of functional place in a dynamic community—mainly but not exclusively in regard to food-habits. Ch. 3 is about limiting factors and the tolerance capacity of animals. It deliberately omits a detailed description of individual 'factors', which is refreshing. There is a remark that 'the search for real limiting factors is rarely a simple or easy job', to which the field ecologist's fervent reply will be 'You're telling me!'

Ch. 4 is called, fairly cumbrously, 'Principles and concepts pertaining to energy in ecological systems'. This is a rather misleading title for a disquisition that includes the food-chain, the pyramid of numbers and productivity. We might say, like Browning:

> Framework which waits for a picture to frame:
> What of the leafage, what of the flower?

Surely it is impossible to treat the food-chain as if the only important feature of it was the intermittent transfer of energy between its species links. The transfer certainly maintains the dynamic changes in the system, it is kept going by sunlight, and of course the supply of energy and its distribution through organic links and channels in nature are fundamental things in ecology. But the energy, after being captured by plants, is carried in the bodies of organisms or their excretory and decay fragments, and these organisms act in a population system that can be studied from a great many, indeed infinitely complex, aspects that do not require energy concepts at all. Odum has, I believe, slightly confused two principles (1) that energy transfer keeps populations going, (2) that living bodies (which are made by the selection and concentration of substances that also eventually become transferred elsewhere) are not a good measure of energy flow or energy transfer. Both these principles are true, but they do not diminish the usefulness of demographic data in the measurement of productivity in populations. I therefore disagree with the author's statement that 'the pyramid of numbers is not very fundamental or instructive as an illustrative device since the relative effect of the "geometric" factor and the "food chain" factor is not indicated'. By 'geometric factor' he means the metabolic throughput of which the biomass is not a direct measure. I have worked out a theoretical method of reconciling these two principles by combining demographic and chemical measurements, which cannot be dealt with here.

There are some most interesting attempts to present the features of the pyramid of numbers, biomass and energy consumption; and some widespread misinterpretations of the idea are corrected. The examples given require scrutiny, since so few exist, and the difficulty of giving true ones is obviously great. I think Petersen's eel-grass food-chain was suggested more as a rough illustration of an idea, than as a reliable set of figures. Similarly, Lindeman's calculations about productivity in the communities in Cedar Lake were guesses rather than reliable facts, since he was compelled to overcome the trouble about converting numbers and biomass into energy consumption, by inserting some very rough corrections for the rate of generation turn-over, and he did not make any allowance for the differences in metabolic rate in different kinds of animals. His conclusions are, to say the least, a shot in the dark. Again, the interesting food-chain 'alfalfa-calf-boy', with its calculated efficiencies at different stages, is not clearly

explained. The efficiency figure for photosynthesis in the alfalfa does not seem to be directly comparable with those in the animal levels. It is given as $6{\cdot}3 \times 10^{10}$ kg. cal. per 10 acres per year. This would seem to represent the primary intake of solar energy by the plants, not the realized efficiency at the end of the complex photosynthetic process. It is no criticism of the author to add that the present stage of this branch of ecology, admittedly a fundamental one, is indicated by the presence of such an example in a text-book: it deals with the amount of beef (and he lives on nothing else) consumed per year by one 12-year old boy! Natural communities are often composed of several hundred species, interlocked in one way or another.

Chs. 5–8 (123 pages) are concerned with populations and communities, from the general point of view. Apart from the valuable chapters in the middle of 'Principles of Animal Ecology' (Allee *et al.* 1949) and some technical monographs, there has not so far been any really good summary of the modern ideas about population structure, components of increase and decrease, fluctuations, regulation and dispersion. On these counts alone this book is worth buying. There seem to be few errors in the treatment of population principles, though it would be expecting too much of any ecologist if all his views about the operation of density-dependent processes received general approval. As an introduction to the subjects named, the book is excellent. The examples are often from recent work, and this gives a freshness to the explanations. The subdivision of interspecific relationships into seven main types (p. 166) is well done, but there is a small mistake in the equation on p. 167, in which $CN_2\ ^2N$ should be CN_2N.

The community concepts do not diverge much from those generally current in America, but good use is made of the available material. It is valuable to read that the gradation of communities into one another 'in no way negates the community concept'. That is to say, the ecologist's job is to study the species network wherever it occurs, though he does in practice tend to choose places where its pattern is relatively stable and uniform, if he is to get down to deeper analytic study. The attitude towards classification of community types is sensible. 'Community names, like names for anything else, should be meaningful but kept as short as possible; otherwise the names will not be used.' He adds: 'Communities, as well as organisms, need to have descriptions as well as names.'

As already indicated, Part 2, though clear and succinct, does not break much new ground. It describes in turn Fresh-water, Marine and Terrestrial Ecology. As in all other ecology books, the terrestrial communities are given a very brief treatment. There is room for a more comprehensive text-book on this subject, after the style of W. Kühnelt's more limited 'Bodenbiologie' (1950).

The bibliography contains a remarkably good proportion of good and new publications (though not Kühnelt's book, in fact practically nothing that is not in the English language). There is an index which also contains a guide to the whereabouts in the text of the explanation of terms and concepts.

I strongly recommend this book, not only to individual research workers and laboratories, but to zoology departments and perhaps even to some schools. C. S. ELTON

WILDLIFE MANAGEMENT IN ALASKA

A. Starker Leopold and F. Fraser Darling (1953). *Wildlife in Alaska.* Pp. ix + 129; 16 plates, 6 maps. New York: Ronald Press Company. Price $2.75.

In 1952 Dr Starker Leopold and Dr Fraser Darling, sponsored by the Conservative Foundation and the New York Zoological Society, spent four months travelling through Alaska to study problems of big-game management. This book gives an account of their journey and of the country and its inhabitants, and sets out the authors' opinions on the ways in which Alaskan wild life should be conserved and exploited. In Alaska the resources of the land are still largely intact and are for the most part the property of the Government of the United States so that, as Dr Fairfield Osborn says in the preface, 'the situation presents a unique opportunity to initiate a comprehensive conservation program before the territory is subjected to haphazard development'.

The most important species reviewed are the caribou, the reindeer and the moose; in all of them the most pressing problem is that of range management and the provision of adequate winter feed. The caribou, formerly distributed throughout Alaska, is now seriously restricted

in range, especially in the southern part of the territory, and the total population in Alaska is estimated to be now about 160,000 whereas in the early 1920's one of the southern herds alone was estimated at over half a million. Some loss is due to the effects of hunting and of predators, but by far the most serious factor has been the loss of the feed on the winter ranges. The caribou is dependent for its winter food almost entirely on the climax vegetation of lichens which are of very slow growth. During the last fifty years vast areas of the winter range have been destroyed by fire—the marauding human population brought to the country by the gold rushes was as completely indifferent to the destructive effects of its activities on the land as the walrus-hunters of the late nineteenth century had been to the decimation of the Eskimos by starvation through the destruction of the main item in their economy. It was in order to provide a new food resource for the Eskimo that reindeer were introduced in the 1890's; in the forty years from 1892 to 1932 the reindeer population had increased from 143 animals to 650,000, and the industry had got out of control. The reindeer completed by overgrazing the process that fire had begun—the destruction of the winter feed of lichens. As a result not only were the caribou banished from the grazings but the reindeer themselves suffered an enormous and spectacular 'crash' in numbers between 1936 and 1948, so that the population now totals only some 25,000 head. North of the Arctic Circle, however, where the range has escaped these destructive influences, the caribou seem to be as abundant as ever they were.

There is no prospect of restoring the reindeer industry or the former abundance of the caribou in the near future. The growth-rate of the arctic lichens is no more than about one-sixteenth of an inch a year and where the lichens have been destroyed it may well take half a century or more to restore the climax vegetation—the Lapp reindeer herders do not graze the same winter range areas more than once in ten years. The authors emphasize again and again that 'the big problem in caribou management is the preservation of the range and not control of decimating factors, such as hunting and predation, which have been getting most of the attention... the problems of caribou management need much more study... both of the animals and their ranges'.

The status of the moose is very different, for the changes in Alaskan vegetation have favoured the spread of willow, birch and aspen which are the critical winter foods of this species. Moose populations are consequently in general increasing both in density and in the areas they occupy. Indeed, the elimination of predators and the regulation of hunting have produced local populations that are as great as, or even greater than, the territories can support, and the authors suggest that the population is being under-harvested and would benefit by the taking of a heavier annual crop.

A short chapter is devoted to some other species, the black-tailed deer of southern Alaska, the Dall sheep, the mountain goat, the re-introduced musk ox, and the introduced elk and bison. The status of none of these animals appears to be in danger, and only one of them, the black-tailed deer, can be considered a major big-game species.

The final chapter deals with the broad principles of wild-life management and with the relationship of big game to the development of Alaska. The authors emphasize that Alaska is 'predominantly a barren and unproductive region in terms of its capacity to support agriculture, industry or high taxes'. The existing exploitable resources, principally fish, timber and water power, should be utilized to the utmost, but in their view the values 'which already exist on much of the Territory—wild fish and game, and the opportunity for wilderness recreation—offer the highest use to which the land can be put'. They reiterate the importance of the preservation of winter range, and emphasize the necessity for further research on all the animals and their ecology, and for the co-ordination of the activities of the various Government services which have already accomplished so much. There is the chance in Alaska to make game management a primary industry rather than a subsidiary adjunct of more intensive forms of land-use.

The authors have written a most interesting and stimulating book; their zoological colleagues will envy them the opportunity they have had for visiting such a fascinating part of the world, and congratulate them on producing such a valuable report on their investigations.

L. HARRISON MATTHEWS

THE MULE DEER

Jean M. Linsdale and P. Quentin Tomich (1953). *A Herd of Mule Deer: A Record of Observations Made on the Hastings Natural History Reservation.* Pp. xiii + 567; 4 plates, 174 text-figures. Berkeley and Los Angeles: University of California Press; London: Cambridge University Press. Price 64*s*.

There is much more than a resemblance in title between this and Fraser Darling's well-known work *A Herd of Red Deer*. This of course is inevitable and implies no reflexion on the authors of *A Herd of Mule Deer*. Their book not only resembles Darling's but in many ways differs from it, not least in being composed largely of the elaborate and meticulous assemblage of detail that one has come to expect in many American field studies of this kind.

The aim of the authors indeed seems to have been to put on record practically every fact observed during their prolonged and careful study of this species. Thus they devote five pages to cestode and nematode parasites found in the mule deer (and many more pages to other animals which may be in any way associated with the deer alive or dead). On the other hand, Darling (whose book is subtitled *A Study of Animal Behaviour*), under the heading 'Helminth Parasites', simply gives references to the literature and observes that it is not his purpose 'to enter into details of factors in the life of the red deer which do not affect their behaviour. As far as I have been able to observe, helminth parasites do not enter into the consciousness of red deer and do not influence behaviour.' The present work has also a long chapter on structure, in which among other subjects growth, variation, and disease in the antlers and in the teeth are discussed and illustrated in detail.

Behaviour too is of course dealt with in all its aspects. The authors consider that 'For the purpose of demonstrating the deer's many responses to a wide range of environmental situations in one locality, a series of examples provides a better understanding than would the combined treatments of them or an attempt to select typical responses.' While appreciating the desire to record all relevant facts, one can only hope that the procedure here adopted will not produce in the reader, as it has sometimes done in the reviewer, an inability to see the herd for the deer.

The chapter-headings are Introduction, Structure, Communication, Mannerisms, Relations to Other Animals, Habitat, Activity, Food, Reproduction, and Population. A large body of precise information is presented on all these themes, as studied among the mule deer on the Hastings Reservation in California—a diversified area of about 1600 acres, protected since 1937 from interference by man, his machines and his domestic stock. There is also perhaps rather much information of the type given in the following passage: 'Wind, soft shoes, wet litter, soft snow, rain, or falling snow all lend a screening or muffling effect to the sounds of a walking man. A stalker's progress into the wind or across it toward deer is certain to prevent his being detected by means of scent. Bushes, trees, ridges, rocks, or an approach from behind are all effective in preventing sight of the stalker by the deer.'

The plates and text-figures are of a high standard. It seems rather surprising that no maps or plans showing the location and general topography of the Hastings Reservation are among them.

COLIN MATHESON

BIRDS

James Fisher (1952). *The Fulmar.* Pp. xv + 496: 4 coloured and 48 black-and-white plates; 55 text-figures. London: Collins (New Naturalist Series). Price 35*s*.

Fulmarus glacialis glacialis, the Atlantic fulmar, is a species notable for both extension of breeding range and increase in population in the last 200 years. Confined, so far as can be ascertained, at the beginning of the eighteenth century to a few colonies in the Arctic and sub-arctic, with one southerly outlier in the St Kilda group, the species has now founded many new colonies in the propinquity of its ancient haunts, colonized the Faeroe Islands (where it first appeared at the beginning of the nineteenth century) and spread to the southern tip of the British Isles.

The documentation of this remarkable and steady increase is the main purpose of Mr Fisher's book. An immense amount of research has gone into the detailed account of the progress of the fulmar along the coasts of western Europe. Arguments are produced that the colonies of Iceland formed the centre whence this spread has taken place, for 'there is no real indication that the fulmar numbers changed on St Kilda while the fowlers were in full activity or after the marked

reduction in human population (in 1922)' and the increase of the population of fulmars along the British coasts was too swift to be accounted for by the breeding of the first pioneers which established themselves outside the St Kilda group in 1878.

The fulmar is interesting in its double ecological relationship with another species—man. Until well into the present century men were predatory upon the fulmar at most of its largest colonies. In the Westmann Islands an average of more than 20,000 young was taken each year in the last decade of the nineteenth century, and about 10,000 a year down to the thirties of the present century. In the Faeroes the maximum harvest was about 4000 young, and in St Kilda in the second half of the nineteenth century the annual catch was something under 10,000, and was about 4000 in 1929 just before the evacuation of the islands. In Iceland fear of psittacosis has led to the banning of the harvest of young fulmars: at the same time egg-gathering was legalized, and the more frequent disturbance of the nesting sites which egging entails has been followed by a marked decrease in the population of the great colonies of the Westmann Islands.

Man is not only predator, he is also provider of food. Mr Fisher discusses at length the effects of first whaling and then trawling upon the fulmar population, and concludes that it is symbiosis with man which has for the present, minimized for this species one of the three great checks upon increase—starvation.

Though Mr Fisher's main care has been to record the spread of the fulmar, the book considers many other aspects of the natural history of the species and of its allies, *F. g. rodgersii* and *F. glacialoides*. In its yearly breeding cycle the fulmar is little affected by latitude: the breeding season at all colonies south of the ice seems to be much the same.

In a book so long it is scarcely surprising that there is a certain inconsistency of treatment. There is much about man as predator in the St Kilda group, but little about Eskimo hunters: the fact that the Eskimo name for one of the Greenland fulmar colonies means 'the place where one shares' offers a fascinating basis for speculation on the sociology of a predatory species capable of reasoning! It may be wished that the documentation of the part played by the modern trawling industry in the increase of this species were as full as the documentation of the geographical details of the spread of the breeding colonies. If the book be difficult to read straight through—it is probably not the author's intention that it should be—this reflects no decline in precision or enthusiasm on the part of the author in the course of its length, but simply the wealth of detail. Should the fulmar continue to increase in times to come, or should there be a period of recession, Mr Fisher has provided the basis for all future studies of advance or retreat.

P. H. T. HARTLEY

James Fisher and R. M. Lockley (1954). *Sea-birds: An Introduction to the Natural History of the Sea-Birds of the North Atlantic.* Pp. xvi + 320; 48 plates; 55 text-figures. London: Collins (New Naturalist Series). Price 25*s*.

This book by two prominent naturalists, on the sea-birds of the North Atlantic and Arctic, contains much that is of interest to the ecologist in connexion with the distribution, population sizes and changes, and life-histories of sea-birds. There is a general survey of the distribution of breeding communities extending from the equator into the High Arctic. It appears from the excellent appendix and a confusing table (p. 24), that of the 116 species, 55 are common to both east and west coasts, if arctic species are included in both, and the remainder are shared more or less equally. The unshared species are mostly grouped in congeneric pairs occupying corresponding niches on opposite sides of the Atlantic. Scattered throughout the book are about fifty valuable maps (unindexed) of breeding distribution. The authors have applied great ingenuity in adapting various map projections for their purpose, although its application is at the expense of clarity in some of the diagrams. A consideration of the world distribution of the main families reveals in most cases a concentration of species in other parts than the North Atlantic, with only two genera and thirteen species peculiar to the area. On this basis it does not seem to have been the centre of any great evolutionary changes except that the gulls (Larinae) and the auks (Alcidae) seem to have spread from arctic waters. It is also useful to students to have the data on the distribution of the various polymorphic species—guillemot, fulmar and the skuas—collected together.

As a result of the rather localized breeding stations of most sea-birds, some remarkable population counts have been possible, in several of which the authors themselves have been involved.

Estimates of world population (breeding pairs) are available for five species: *Puffinus gravis* (only casual visitors to the area), 2–2½ million; *Pterodroma cahow*, *c.* 100; *Pelecanus erythrorhynchos*, *c.* 15,000; *Sula bassana*, *c.* 83,000; *Fratercula arctica*, 7–8 million. And partial censuses for thirty-one other species are summarized. Either the little auk or Brünnich's guillemot is the most abundant species of the north, the largest known colony of the former, on Greenland, being estimated at 5 million. There is careful documentation of certain changes in local and world populations, notably of the great auk, the gannet and some tern species. The most detailed data, on the recent southward spread of the fulmar, have been presented by one of the authors in a previous book.

The discussion of factors controlling sea-bird populations is more controversial, for concrete data are only available for one factor, human predation. Fecundity, longevity and exchange between populations receive little attention, and until these are well known, the impression made by human predation, which the authors believe 'most importantly controls the number of sea-birds', cannot be assessed. Even in some cases of extinction it is difficult to be sure whether man has been the prime factor, or has just assisted a decline already begun, though he must be held responsible for the demise of the great auk. Food as a controlling factor is discussed. The interesting suggestion, put forward previously by Mr Fisher, that the spread of the fulmar is related to the disposal of whale and fish offal at sea, is repeated. Several illustrations of Gause's principle are given. The shag and the cormorant, for example, take different fish in the same area, and even in the superabundance of arctic plankton the sea-birds seem to take different foods. It is concluded that 'wherever the ecology of—cohabiting—species has been intensively studied, real differences in food patterns are apparent'. Nest sites are also dissimilar in some way even between species so alike in general preference as common and Brünnich's guillemots. The Fraser Darling effect, never quite satisfactorily established, is again put forward without further evidence, which is a pity in view of the opportunities which must have occurred for study. The authors are led to the general conclusion that 'numbers depend primarily on food', but that 'not all species are—even in the breeding season—at the limits of their food supply'. This seems to be premature, for there is no unambiguous evidence for either of these, as general statements.

There are chapters on movements and navigation which, although containing interesting information, are diffuse and select rather arbitrarily from available data. The last half of the book consists of life-histories of the six main families. In some cases it is not made clear which species is being discussed, as in the chapter on terns, but there is a great range of valuable data which it is impossible to summarize here. To give just two examples; other petrels are shown to have the incredibly long incubation and fledgling periods of the Manx shearwater; and the history of the search for the breeding place of Ross's gull, found in 1905, makes fascinating reading. Inevitably some aspects are neglected, and social behaviour is one of these. Especially one may regret the separate chapter on this subject where there is little that has not been better dealt with by other workers, even the most important of whom do not seem to have been referred to by the present authors. But the great assembly of data on other aspects makes this book a significant contribution to the study of sea-birds.

P. MARLER

Roger Peterson, Guy Mountfort and P. A. D. Hollom (1954). *A Field Guide to the Birds of Britain and Europe*. Pp. xxxiv + 318; 64 plates (40 of them in colour); numerous text-figures including 380 distribution maps. London: Collins. Price 25*s*.

This is a remarkable little book, and singularly fascinating from one to the other of its end-papers showing silhouettes of common birds. As its overall dimensions are $7\frac{1}{2} \times 4\frac{7}{8} \times \frac{7}{8}$ in., it will go comfortably into an ordinary pocket. Within this small compass are concise but surprisingly full descriptions of more than 500 species of bird normally occurring in Britain and Europe including Scandinavia, together with small but clear distribution maps for most of them. A final section deals more briefly with 100 'accidentals' defined as species recorded less than twenty times. An admirable introductory chapter on 'How to Identify Birds' is followed by an eminently sane note on 'The Problem of Subspecies' and a check-list. The arrangement of the book is taxonomic but based on English names (scientific names are also given). The description of each species includes vernacular names in Dutch, German, French and Swedish, and brief

notes on habitat. The striking feature, however, is the admirable illustrations. For a great many species there is in addition to a conventional side view in colour a drawing in monochrome of the bird in flight. In some of the more difficult groups there are additional plates showing, for example, the ducks in flight as seen both from above and from below, the details of the heads of terns, or the immature plumage of the gulls. In all the plates attention is drawn to the diagnostic features, which are also the subject of notes on the opposite page.

The authors and publishers are much to be commended for producing a book so well designed for its purpose and for transcending national boundaries in doing so. H. C. GILSON

BOOKS RECEIVED

Information Theory in Biology. By HENRY QUASTLER (editor). Urbana, Ill.: University of Illinois Press. 1953. (No price given.)

Birds as Animals. I. *A History of Birds*. By JAMES FISHER. London: Hutchinson's University Library. 1954. Price 8*s*. 6*d*.

Principles of Biochemistry: A Biological Approach. By M. V. TRACEY. London: Pitman. 1954. Price 20*s*.

Microbiology: an Introduction. By ERNEST GRAY. London: Crosby Lockwood. 1954. Price 10*s*. 6*d*.

The Struggle for Existence. By UMBERTO D'ANCONA translated by ANNE CHARLES and R. F. J. WITHERS. Leiden: E. J. Brill. 1954. (No price given.)

The Heron. By FRANK A. LOWE. London: Collins (New Naturalist special volume). 1954. Price 18*s*.

The Western End of Lake Erie and its Ecology. By THOMAS H. LANGLOIS. Ann Arbor Mich.: Edwards. 1954. Price $10.00.

ABSTRACTS

The abstracts are edited by Prof. L. A. Harvey with the assistance in selection and abstracting of J. D. Brayshaw, D. H. Chitty, G. I. Crawford, A. E. Ellis, P. D. Gabbutt, Miss U. Grigg, N. A. Holme, A. Macfadyen, C. Matheson, Miss E. Nelmes, G. G. Vickers and M. Williamson. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations can greatly aid this work by making sure that copies of their publications are sent regularly to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** It has recently become noticeable that some organizations have sent their material only at irregular intervals. Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Prof. L. A. Harvey, University College, Exeter.** In view of the list of journals from which it is at present impossible to provide abstracts, the services of several new volunteers will be very welcome.

Separate copies of the abstracts can be obtained from **The Cambridge University Press, 200 Euston Road, London, N.W. 1,** or through any bookseller; price 5*s.* 6*d.* per annum, post free (issued in May and November). Back numbers of the 'Notices of publications...' from Vol. 3 (1934) to Vol. 20 (1951) may also be held at 2*s.* for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *Bird Notes* and *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above two journals and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Barnes, H. & Powell, H. T. (1953). The growth of *Balanus balanoides* (L.) and *B. crenatus* (Brug.) under varying conditions of submersion. *J. Mar. Biol. Ass. U.K.* **32**, 107–27.

Settlement and growth on experimental panels, exposed at various levels on the shore and constantly submerged, are recorded. Length/breadth ratios vary with age of the individual and with intertidal level. A suggested cause of the heavier settlement of *B. balanoides* at mid-tide level is given.

Gauld, D. T., Bagenal, T. B. & Connell, J. H. (1953). The marine fauna and flora of St. Kilda. *Scot. Nat.* **65**, 29–49.

An account of zonation on rocky shores, the fauna of a sandy beach, together with a list of marine animals and plants taken on the shore and by dredging.

Harris, J. E. (1953). Physical factors involved in the vertical migration of plankton. *Quart. J. Micr. Sci.* **94** (4) 537–50.

The mechanism of light response in *Daphnia* and other species suggests that vertical migration is an inescapable consequence of the use of light by planktonic forms as a means of attaining a level within the euphotic zone.

Holme, N. A. (1953). The biomass of the bottom fauna in the English Channel off Plymouth. *J. Mar. Biol. Ass. U.K.* **32**, 1–49.

A survey of the macrobenthos at twenty stations off Plymouth. Sources of error in sampling are considered in detail, and some data are given on the size of sample necessary for an evaluation of the bottom fauna at a station. The dry weight of living tissue at each station is given, the mean for all stations being 11·2 g./m.^{2}. Comparison with a previous survey in 1922–23 indicates a decline in numbers of the bottom fauna.

Marcus, E. & Macnae, W. (1954). Architomy in a species of *Convoluta*. *Nature, Lond.* **173**, 130.

Owen, G. (1953). On the biology of *Glossus humanus* (L.) (*Isocardia cor* Lam.). *J. Mar. Biol. Ass. U.K.* **32**, 85–106.

An account of the structure of this lamellibranch in relation to its habitat in deep water muds.

Segal, E., Rao, K. P. & James, T. W. (1953). Rate of activity as a function of intertidal height within populations of some littoral Molluscs. *Nature, Lond.* **172**, 1108–9.

Using a described method it is shown for two species of limpet, that the lower they are collected in the intertidal zone, the higher the rate of heart beat. The same relationship exists when the rate of propulsion of water is estimated in a named mussel. The relation between intertidal and latitudinal distribution is discussed.

Wilson, D. P. (1953). The settlement of *Ophelia bicornis* Savigny larvae. The 1952 experiments. *J. Mar. Biol. Ass. U.K.* **32**, 209–33.

Further work on settlement shows that the attractive properties of certain sands may be transferred to other media, but the transference of the repellent factor was not so clearly demonstrable. Activated charcoal stimulates settlement. Grade size of the sand is again shown to influence settlement.

(*b*) Fresh Water

Longhurst, A. R. (1954). Reproduction in Notostraca (Crustacea). *Nature, Lond.* **173**, 781–2.

Reports the occurrence of functional testis in the gonads of all specimens examined of the so-called parthenogenetic races of *Triopa* (=*Apus*) *cancriformis*. This phenomenon is also reported from other members of the Notostraca.

(*c*) Land

Basden, E. B. (1953). The autumn flush of *Drosophila* (Diptera). *Nature, Lond.* **172**, 1155–6.

Collections made in three successive years suggest that the autumn flush is an annual phenomenon in the Edinburgh region. Ten species are recorded, but the increase was due mainly to *Drosophila subobscura*.

Phillips, N. R. (1953). Fauna of a decaying log and the life-cycle of *Helops caeruleus* (L.) (Col., Tenebrionidae). *Entomologist*, **86**, 226–8.

Of the eight Arthropods recorded on a log that had been exposed for three years on arable land, only larvae of *H. caeruleus* fed directly on the log itself. Predation on the immature stages by *Lithobius* and possibly *Lasius* maintained the population of this Tenebrionid at an approximately even level.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Bailey, N. T. J. (1953). The use of chain-binomials with a variable chance of infection for the analysis of intra-household epidemics. *Biometrika*, **40**, 279–86.

Adopts Greenwood's suggestion that there is a binomial distribution of secondary cases from contact with primary cases, and tertiary cases from secondary, and that the average chance of infection varies from household to household in diseases, like measles, with short periods of high infectivity. The observed course of a measles epidemic is fitted excellently by the model.

Darwin, J. H. (1953). Population differences between species growing according to simple birth and death processes. *Biometrika*, **40**, 370–82.

Considers the mathematical relation between birth- and death-rates and population size necessary to produce various theoretical distributions of the frequency of different species in a sample. Equations are also found for the distribution of a group of species in a series of localities, the probability of a given species becoming established in a given area being derived from population size, and these give a good fit to some Hawaiian data.

Eastop, V. F. (1953). A study of the Tramini (Homoptera–Aphididae). *Trans. R. Ent. Soc. Lond.* **104**, 385–413.

With key to most of the British species and host plant list.

Forster, G. R. (1953). A new dredge for collecting burrowing animals. *J. Mar. Biol. Ass. U.K.* **32**, 193–8.

A lightly built dredge, capable of digging deeply into sand or mud, is described. Comparative tests against other dredges show that the new dredge is a more efficient instrument for capturing members of the burrowing fauna.

Freeman, G. H. (1953). Spread of diseases in a rectangular plantation with vacancies. *Biometrika*, **40**, 287–96.

In a hop plantation diseased plants occur next to one another more often than would be expected by chance. Healthy plants next to diseased plants are more likely to be diseased the following year than those next only to other healthy plants. The mathematical problems involved are fully discussed.

Gilbert, O. (1954). Field life-histories of four species of *Calathus* (Coleoptera, Carabidae). *Nature, Lond.* **173**, 731–2.

Life-histories of *Calathus erratus*, *C. fuscipes*, *C. mollis* and *C. melanocephalus* from samples taken on dunes in Anglesey.

Good, I. J. (1953). The population frequencies of species and the estimation of population parameters. *Biometrika*, **40**, 237–64.

The estimation of the expected frequency of any species and of the total number of species in a population using the distribution of the number of species observed 1, ..., n times. The estimates are derived either from curves fitted to the data in accordance with one of nine hypotheses, or from the original observations after they have been smoothed severely.

Hammad, S. M. (1953). The immature stages of *Metophthalmus serripennis* Broun (Coleoptera: Lathridiidae). *Proc. R. Ent. Soc. Lond.* (A), **28**, 133–8.

An account of the life-history together with a description of the external morphology of the immature stages.

Hammersley, J. M. (1953). Capture-recapture analysis. *Biometrika*, **40**, 265–78.

A fully stochastic model, avoiding all theoretical difficulties other than that each sample must be random and that the chance of death of one individual is not affected by other individuals. The method measures the likelihood of the successive recaptures of each individual, rather than the likelihood of the recaptures observed at any one time. As this gives more unknown parameters than equations, to get unique solutions it is assumed that the death-rate at any one time is the same for all individuals. The method is applied to a population of alpine swifts sampled once a year for 30 years. The calculations would have taken 8 months on a desk machine.

Hansen-Melander, E., Melander, V., & Reynoldson, T. B. (1954). A new species of fresh-water Triclad belonging to the genus *Polycelis*. *Nature, Lond.* **173**, 354–5.

In western Europe this genus contains three species, *Polycelis nigra*, *P. tenuis* and *P. hepta* n.sp.— separated by the structure of the copulatory organs and the number of chromosomes. The geographical range of the species is indicated.

Hickin, N. E. (1953). Larvae of the British Trichoptera. 40. *Proc. R. Ent. Soc. Lond.* (A) **28**, 163–5.

The larva of *Micropterna sequax* (Limnephilidae) is figured and described.

Kimmins, D. E. (1953). A key to the European species of *Wormaldia* (Trichoptera, Philopotamidae), with descriptions of two new subspecies. *Ann. Mag. Nat. Hist.* (12) **6**, 801–8.

With drawings of the male genitalia for all European species and subspecies, including the four British species.

Long, D. B. (1953). Effects of population density on larvae of Lepidoptera. *Trans. R. Ent. Soc. Lond.* **104**, 543–91.

Ten species (*Diataraxia oleracea*, *Orthosia cruda*, *O. gothica*, *O. incerta*, *O. stabilis*, *Pieris brassicae*, *Plusia gamma*, *Saturnia pavonia*, *Dilina tiliae*, *Laothoe populi*) were used in experimental work to determine the effects of population density by comparing solitary larvae with those bred in crowded cultures. Seven species showed differences in larval colour, the crowded larvae being generally darker than the solitary ones. The effects on morphology and histology are described and illustrated. Crowding has a number of effects: it increases the rate of development; the larvae have fewer instars; there is a more simultaneous pupation; a low pupal weight and low larval mortality. Behaviour was most important. In *P. gamma* crowded larvae were four times more active and spent 25 % more time feeding than solitary stages. These results are compared with those obtained from the phases of locusts.

Millidge, A. F. (1954). On a new species and genus of spider. *Ann. Mag. Nat. Hist.* (12) **7**, 253–6.

Praestigia duffeyi (Linyphiidae) from pure *Halimione portulacoides* saltmarsh on Havergate Island.

Southwood, T. R. E. (1953). The morphology and taxonomy of the genus *Orthotylus* Fieber (Hem., Miridae), with special reference to the British species. *Trans. R. Ent. Soc. Lond.* **104**, 415–49.

A check-list and a key to the British species.

3. PARASITES

Dunn, E. (1954). Factors influencing the emergence of *Heterodera rostochiensis* larvae. *Nature, Lond.* **173**, 780.

The rate and amount of hatching from viable cysts of the same age maintained at 15° C. is profoundly affected by the maximum temperatures to which the moist cysts have been subjected previously.

Muir, D. A. (1954). Ants *Myrmica rubra* L. and *M. scabrinodis* Nylander as intermediate hosts of a cestode. *Nature, Lond.* **173**, 688–9.

A description of the cysticercoids is given, and it is suggested that they may be intermediate stages of *Raillietina* (*Paroniella*) *urogalli* which infects the red grouse *Lagopus scoticus scoticus*.

Owen, D. F. (1953). *Protocalliphora azurea* Fall. in birds' nests with a record of the killing of magpie nestlings by the larvae of this fly. *Ent. Rec.* **65**, 267.

In 1953, only one great tit's nest of thirty-five tit's nests and two redstart's nests examined was infested, whereas twenty infested nests were found in the same area in 1952. Whitethroat and magpie are recorded as hosts for the first time. A nest in which three magpie nestlings died, one certainly owing to larval attack, was subsequently found to contain 250 larvae.

Pike, R. B. (1953). The bopyrid parasites of the Anomura from British and Irish waters. *J. Linn. Soc. (Zool.)* **42**, 219–37.

Contains records of the occurrence and hosts of bopyrid parasites. Each species of parasite usually restricts itself to a single host species.

Thompson, G. B. (1954). Contributions towards a study of the ectoparasites of British birds and mammals. No. 2. *Ann. Mag. Nat. Hist.* (12) **7**, 17–39.

Ornithomyia (Diptera, Hippoboscidae): identification, life-history, recorded hosts, British distribution, percentage of birds parasitized, and as carriers of Mallophaga and Acarina parasitic on birds. Two species recognized: *avicularia* and *fringillina*, the latter including *lagapodis* as a synonym. Both species recorded from many hosts, about one-third of the hosts are attacked by both, although certain families are chiefly attacked by one species. Both species are most common in August.

4. FOOD AND FOOD HABITS

Buxton, P. A. & Barnes, H. F. (1953). British Diptera associated with fungi. 1. Gall midges (Cecidomyidae) reared from the larger fungi. *Proc. R. Ent. Soc. Lond.* (B) **22**, 195–200.

A description of the males, females and larvae of *Camptodiplosis auriculariae* n.sp. obtained from *Auricularia auricula-judae* is provided, together with notes on three more provisionally identified species new to the British list.

Laurence, B. R. (1953). On the feeding habits of *Clinocera* (*Wiedemannia*) *bistigma* Curtis (Diptera: Empididae). *Proc. R. Ent. Soc. Lond.* (A) **28**, 139–44.

Feeds on dead insects trapped in the water film.

Laurence, B. R. (1953). Observations on *Hemerodromia unilineata* Zett. (Dipt., Empididae). *Ent. Rec.* **65**, 299–300.

Prey of males in Shropshire comprised *Tanytarsus* sp., *Pericoma* sp. and two undetermined Chironomids. A Braconid and a Psychodid were attacked unsuccessfully, but Aphids, which were numerous, were not attacked. A female *Chelifera precatoria* preyed on a Chironomid.

Shelbourne, J. E. (1953). The feeding habits of plaice post-larvae in the Southern Bight. *J. Mar. Biol. Ass. U.K.* **32**, 149–60.

The post-larvae appear to be feeding selectively on *Oikopleura dioica*.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Bagenal, T. B. (1954). *Ophiocten scutatum* Koehler at St Kilda. *Ann. Mag. Nat. Hist.* (12) **7**, 143–4.

Two specimens of this brittle star were found in 10–15 m. The fourteen specimens previously known had been found in 88–160 m.

Bevan, K. (1954). Notes on the Macrolepidoptera of the Fylde coastal area of West Lancashire. *Ent. Rec.* **66**, 74–7.

A list from an area of sand-dunes threatened with elimination by building operations, with notes on numbers and, in some cases, food plants.

Clark, R. B. (1953). *Lumbrinereis cluthensis*, n.sp. (Eunicidae), a new polychaete from the Firth of Clyde. *Ann. Mag. Nat. Hist.* (12) **6**, 945–9.

In fine mud at 90 m.

Cole, H. A. & Baird, R. H. (1953). The American Slipper Limpet (*Crepidula fornicata*) in Milford Haven. *Nature, Lond.* **172**, 687.

Collingwood, C. A. (1953). Ants in Galloway. *Ent. Rec.* **65**, 297–8.

Seven new records for Kirkcudbrightshire and eight for Wigtownshire.

Fonseca, E. C. M. d'Assis- (1954). *Syneches muscarius* F. (Empididae), an addition to the British list. *Ent. Rec.* **66**, 121–2.

Recorded from Dorset in 1953.

Fryer, G. & Smyly, W. J. P. (1954). Some remarks on the resting stages of some freshwater cyclopoid and harpacticoid copepods. *Ann. Mag. Nat. Hist.* (12) **7**, 65–72.

Winter dormant stages of three species from the Lake District. *Cyclops bicolor* and *Canthocamptus staphylinus* from the shallow bottom of a tarn, *Cyclops leuckarti* from profundal deposits of two lakes.

Harper, G. W. (1954). The Macrolepidoptera of Inverness-shire—Newtonmore District. *Ent. Rec.* **66**, 58–64, 90–96, 124–8.

A list from an area within a 20-mile radius of Newtonmore, much of which has not been worked systematically, with notes on abundance, habitats and status.

Pitman, C. M. R. (1954). An account of results obtained when breeding *N. io* and *A. urticae* for the purpose of marking and liberating to trace their movements. *Ent. Rec.* **66**, 8–12.

Of 2581 *Nymphalis io* and 1332 *Aglais urticae* released in Wiltshire, thirty-seven and seventy-four, respectively, were captured at distances greater than one mile from the place of release. The distances flown and the number of days before recovery are tabulated. *N. io* tended to fly N.N.E., regardless of wind direction, whereas *A. urticae* tended to remain in the liberation area for a time.

Tebble, N. (1954). On the polychaete *Dasybranchus caducus* (Capitellidae) from British waters. *Ann. Mag. Nat. Hist.* (12) **7**, 316–20.

Identification and records.

Went, A. E. J. & Gibson, F. A. (1953). Salmon movements around Ireland. IV. From Streedagh, Co. Sligo (1951 and 1952). *Proc. R. Irish Acad.* **56**B, 1–12.

Over 80 % of the fish had apparent rates of travel of less than 5 miles per day. Over 90 % travelled less than 50 miles, none more than 100 miles. Data of tagging at Achill and some notes on the tagging of kelts.

Went, A. E. J. & Vickers, K. U. (1953). Salmon movements around Ireland. V. From North County Antrim (1951 and 1952). *Proc. R. Irish Acad.* **56**B, 13–28.

In addition to the usual short movements, about 2 % travelled over 100 miles, one for 410 miles.

White, J. H. (1953). Wind-borne dispersal of potato-root eelworm. *Nature, Lond.* **172**, 686–7.

The use of air traps has shown that there is considerable movement of viable cysts of *Heterodera rostochiensis* in blowing soil.

Woodruffe, G. E. (1953). On the occurrence at Hounslow, Middlesex, of *Metopoplax ditomoides* Costa (Hem., Lygaeidae) new to Britain. *Entomologist*, **86**, 224–5.

Contains a description of *M. ditomoides*, which is also recorded from Jersey.

6. STUDIES ON BEHAVIOUR

Cloudsley-Thompson, J. L. (1953). Studies in diurnal rhythms. IV. Photoperiodism and geotaxis in *Tenebrio molitor* L. (Coleoptera: Tenebrionidae). *Proc. R. Ent. Soc. Lond.* (A) **28**, 117–32.

The distribution of the different stages of this mealworm in bran is regulated by their reactions to light and gravity; adults and full grown larvae are photonegative and negatively geotactic and small larvae are positively geotactic. Their behaviour is compared to that of *Ephestia elutella* and the ecological implications, with especial regard to the emergence and distribution of the adult, are discussed.

Harker, J. E. (1954). Diurnal rhythms in *Periplaneta americana* L. *Nature, Lond.* **173**, 689–90.

Experiments suggest that a secretion is involved in the production of a diurnal rhythm of activity.

Hough, J. S. (1953). A preliminary note on the effect of high and low temperatures on hatching of the adult agamic form of *Neuroterus quercus-baccarum* L. (Hym., Cynipidae). *Entomologist*, **86**, 218–23.

From the rearing experiments described, the author concludes that at temperatures of 1 and 5° C. the emergence of both *N. quercus-baccarum* and its parasites is greatly delayed, that a certain critical development stage must be reached before the larvae can withstand low temperatures, and that although the rate of development increases with increased temperatures, healthy development ceases at temperatures of 25° C. or more.

Johnson, B. (1954). Effect of flight on behaviour of *Aphis fabae* Scop. *Nature, Lond.* **173**, 831–2.

Experiments show that the change from Moericke's *Zugphase* to *Befallsphase* can be brought about by flight itself and that it is not necessarily permanent.

BRITISH ECOLOGICAL SOCIETY

EASTER MEETING AT EDINBURGH

9–10 April 1953

The Easter Meeting of the Society was held at the Royal Botanic Gardens, Edinburgh, by kind courtesy of Prof. Sir William Wright Smith, F.R.S.

9 *April*. The morning session commenced at 10 a.m. when Sir Wright Smith welcomed the Society to Edinburgh. In the absence of the President, the Vice-President of the Society, Prof. A. R. Clapham, took the Chair.

The first paper was given by Dr G. K. Fraser on 'Some topographical features of the Blanket Moss of the north-west of Scotland'. This paper dealt with observations made during a reconnaissance survey of the peat land of the Island of Lewis, from which a general picture of the Blanket Moss of the north-western region of Scotland could be given. Of the total surface of the non-mountainous area of the Island, some 730 square miles, over 80% carries a cover of peat of a general depth of 2 m. increasing to 7½ m. in local hollows. The general vegetation of this was described briefly and reference was made to a few types of particular interest, including some ascribed to manuring by animals.

Emphasis was laid on the evidence of movement in the peat, varying from scarcely detectable mass movement to catastrophic peat 'avalanches' of which a recent example was described. The evidence of shrinkage and subsequent cracking was also referred to, and of the resistance of peat to wind and water erosion as compared with 'frost-lifting' and wind blast, while some particular examples were given of the resistance of peat to simple wind and water erosion. The importance of these factors is, perhaps, not generally recognized in connexion with the development of minor features of peat topography such as hags, flows, lochans and other common features of peat topography.

Interesting features of certain regeneration complexes, in which *Molinia* and *Rhacomitrium* were involved, and the effect on the vegetation of nitrogen manuring by animals were dealt with in the discussion that followed. Those taking part were Prof. A. R. Clapham, Dr J. Hope Simpson and Dr Eville Gorham.

Dr C. B. Goodhart then gave his paper on 'Non-adaptive variation in a population of the snail, *Cepaea nemoralis*'.

A population of this snail living beside the New Bedford River in Cambridgeshire is believed to show non-adaptive variation as a result of genetic drift.

C. nemoralis is abundant on the artificial river bank running straight across the fens, but is absent from the cultivated land beside it, so this population is practically one-dimensional. For 2 miles north of Earith a road runs beside the bank, which is 10 ft. high, built of silt and covered with long grass, slightly grazed towards Earith, but otherwise very uniform. On the other side the road verge slopes down to the fen, with black peat soil and rank vegetation. Thus there is a consistent difference between bank and verge greater at any point across the road than along the whole length of either.

Samples of snails at furlong intervals show considerable genetic variation. Thus brown shells ranged from 0 to 43%, pink 8 to 74%, bandless 0 to 55%, bands dotted 3 to 48%, bands fused 7 to 65%, and so on.

In general populations from either side of the road are similar, despite differences in soil and vegetation, while there are striking changes within a short distance along the bank, without apparent changes in environment.

The main predators are rats and voles, thrushes are absent, and collections of rat-eaten shells gave little evidence of selection. It is concluded that, though colour and banding are selected by birds, where rats are the predators these characters are selectively neutral. Thus in a large but not panmictic population where there is isolation by distance, genetic drift can occur.

A lively discussion ensued in which Prof. Clapham, Dr Riley and Dr P. M. Sheppard took part. Dr Sheppard pointed out that this valuable investigation does not prove that the observed variation is due to genetic drift. The proportions of the different phenotypes at these collecting stations agree with those found by Cain and Sheppard (in manuscript) in rough herbage but not in woods. Consequently selection must be acting. To show that it is the same in all breeding communities it must be proved that the amount of predation is the same in all areas. Moreover, even in identical conditions it is possible to obtain different gene frequencies by selection alone, if the genes affect each other's selective value, which they have been shown to do in *Cepaea*.

Dr C. B. Goodhart replied that the amount of visual predation has not been measured, but the argument is, that pairs of populations on different backgrounds are similar, though there may be marked changes within a few hundred yards without apparent changes in the background. Some ten common phenotypes show these fluctuations, and none have been found constant along the whole bank.

Mr M. C. Pearson followed, giving an account of 'Some aspects of the ecology and history of Muckle Moss, Northumberland'.

The surface vegetation of Muckle Moss consists of two central flush communities influenced by a small inflow of ground water, and a drier marginal community mainly dependent on atmospheric precipitation. Both flush communities are characterized by *Eriophorum angustifolium*, *Erica tetralix* and *Calluna vulgaris* as the dominants and by a complete cover of *Sphagnum* spp. The wetter of the two flushes is partially enclosed by pools of water, some of which are overgrown with various spp. of *Sphagnum*, *Carex* spp. and *Eriophorum angustifolium*. This flush is distinguished by the presence of hummocks of *Polytrichum commune* and *Eriophorum vaginatum*, and hollows forming a distinct mosaic, whereas their distribution in the other flush community is extremely localized (*Sphagnum papillosum* and *S. magellanicum* being the chief hummock builders). Sparsely distributed pine and birch occur only on the wetter flush. The drier marginal community which is characterized by a small number of species, and a poorly developed *Sphagnum* cover, is dominated by tussocked *Eriophorum vaginatum*, *Calluna vulgaris* and *Sphagnum recurvum*. There is some variation due to grazing and burning. There is also a small localized marginal willow carr.

The level of the water table appears to be the most important factor influencing the vegetation and has been shown to be consistently higher throughout the year and less subject to seasonal variation in the flush communities than in the marginal community. The soils of the wetter area have a higher pH (4·5) than the drier parts (pH 3·25). The general features of the surface vegetation show a close affinity with the mixed mire group of bogs of the Scandinavian ecologists.

An examination of the bog deposit has revealed in the deepest part (45 ft.) a stratigraphical sequence from the bottom upwards of clay, detritus mud, brushwood peat, and *Sphagnum-Eriophorum* peat. There has been a change from a eutrophic open water vegetation to the present oligotrophic bog vegetation. Pollen analytical data show that the upper layers of the clay date from Zone V (Godwin) and that the accumulation of peat commenced in Zone VI.

In the discussion that followed Mr P. J. Newbould, Dr Gorham and Prof. Clapham took part.

The morning session terminated with an account by Dr L. W. Poel of 'Some effects of aeration on *Calluna vulgaris* and *Erica tetralix*'.

The growth of *Calluna* in a Crone nutrient solution was favoured by stagnation of the medium, and this was also true to a lesser degree of *Erica tetralix*. Moreover, *Calluna* plants growing in pots containing peaty soil survived total submergence of the pots in water only when the water was left unaerated. These results were contrasted with those previously recorded for *Pteridium* in which healthy growth (and even survival in waterlogged pot cultures) depended upon continuous aeration of the medium.

An account was given of studies of respiratory rate in roots of *Calluna* and *Erica tetralix*, as affected by exposure to air and to commercial nitrogen (containing approximately 0·2% oxygen). Polarographic and manometric methods were used.

In the polarographic experiments, the respiratory rate was measured in phosphate buffer (pH 5·6) immediately following exposure of the roots to one or other of the two oxygen tensions.

From these experiments it was concluded that the rate of respiration tended to be greater after nitrogen pretreatment. Comparable experiments on *Pteridium* were referred to in which respiration was favoured by aeration.

In the manometric experiments it was found that oxygen consumption by the roots of both ericaceous species was initially greater in 0·2% oxygen than in air. Indeed, in *Calluna* there was no measurable oxygen uptake in air during the first 30 min.

It was tentatively suggested that these experiments are in keeping with the observed tolerance by *Calluna* and *Erica tetralix* of poor aeration in the field, although the apparent toxic effect of aeration is less understandable, since *Calluna* is frequently found in well-aerated situations.

These results were of considerable interest and in the ensuing discussion Drs Harley, Gorham and Hughes discussed various points of technique and the general ecological implications of the work.

The afternoon session was opened by Mr P. J. Newbould, who gave an interesting account of the ecology of Cranes Moor, a New Forest bog.

This bog is near Burley, on the western fringe of the Forest, lying in a sandy basin surrounded by acid *Calluna* heath and pine scrub. The variation in surface vegetation is largely controlled by the degree of flushing. The bog system contains two main flushed areas with vegetation dominated either by *Schoenus nigricans*, or by *Myrica* and *Molinia*. Between them in a shielded position is an area dominated by *Sphagnum papillosum* and *Rhynchospora alba*. The annual turn-over per unit area of organic matter, calcium and iron is strikingly greater in the flushed than in the shielded area.

The stratigraphy shows that this difference has been maintained throughout the development of the bog. In the shielded area there is up to 5 m. of *Sphagnum* peat, mostly formed during the Boreal period, by the growth of *S. papillosum*. This was preceded by a little peat formed from *Sphagna* of the sections *cuspidata* and *subsecunda*. At the end of the Boreal, growth almost ceased and the surface vegetation was composed mainly of *Sphagna* of the section *acutifolia*, and of *Calluna*. There has been little subsequent growth of peat, the bog having filled the basin available to it. The southern of the two flushed bogs shows a succession from a shallow lake with *Menyanthes* and *Potamogeton* sp. colonizing, followed by a *Phragmites* reedswamp, with occasional *Cladium*, *Typha* and *Equisetum fluviatile*, and later with scattered birch and willow trees, culminating in the present vegetation of *Schoenus* along the central flush and *Myrica* and *Molinia* marginally. The northern flushed bog is smaller but similar in its general succession. This succession has in both instances been brought about by terrestrialization rather than by chemical change in the flush water.

In reply to Dr McVean, Mr Newbould stated that he could not explain the absence of the alder from this Moor.

Miss S. Y. Barkley gave an enjoyable paper on the 'Sands of Forvie, Aberdeenshire'. It was well illustrated by excellent photographs of the area.

The Sands of Forvie, occupying an area of 3 by 1 miles, and situated 15 miles north of Aberdeen, are an example of a dune system typical of north-west Europe, but as yet undescribed for Britain. The often repeated pattern of vegetation can be closely related to topographic succession in the parallel waves of parabola or 'U' dunes, which comprise the area. The parabolas have an average width of about 1000 ft., and a height of up to 20 ft., their wings being orientated approximately south-west, in alignment with the resultant of sand-moving winds. In the youngest *mobile* parabola phase the leeward deposition slope, which grades gently into the windward erosion slope, is uncolonized or bears scattered *Ammophila arenaria*, *Cirsium arvense*, and *Senecio jacobaea*, giving poor cover and no visible humus layer. In the *mature* phase, where the yearly advance of blown sand is a matter of inches only (compared with advances of up to 150 ft. in a year in the youngest phase), transition between the now steeper windward and leeward slopes is sudden. This knife edge is caused by the deeper layer of humus with resistant roots and rhizomes, and the increased steepness of the windward slope results from the accumulation of sand arrested by the denser vegetation of the previously mentioned species, now augmented by grasses and mosses. In the *deflation* phase erosion and deposition are localized in small hollows in the parabola bow and wing. With the increased general stability vegetation consists of various facies of *Calluna* heath, with *Empetrum nigrum* and *Cladonia sylvatica* as prominent species. Incipient podsolization occurs here, with a bleached A_2 layer, and a B zone of ferric deposition, below the 3–4 in. deep surface humus. Thus with age the three series of vegetation, dune topography and soil profile become increasingly complex, more stable, and closer to the water table. Wherever water table is reached, as in local deflation phase hollows, and in flat plains, between waves of parabolas, colonization by *Juncus* spp., mosses, grasses, *Erica*

tetralix, *Salix repens*, *Empetrum* and *Calluna* occurs, 'wet heath' being the climax community. By reference to buried remains of an Iron Age site, a medieval church foundation, a ridge-and-furrow ploughed field system and a 1782 map, the original sand advance prior to *c.* 50 B.C., and the readvance at present in progress, can be dated.

In the ensuing discussion Dr Hope-Simpson discussed the contrast between parabolic and parallel dunes, the latter involving the movement of larger quantities of sand, which cannot be easily fixed by vegetation, leading to the development of blow outs. Drs Clarke, Gimingham and Gorham also took part in the discussion.

At 8 p.m. on the evening of 9 April, members of the Society were invited to a meeting of the Edinburgh Botanical Society, at the Royal Botanic Garden. Dr Peter Davis gave a lecture on 'Plant life in central and north-eastern Turkey', being an account of his expedition to the Anti-Taurus and Pontic-Taurus in 1952. The lecture was very well illustrated and thoroughly enjoyed by all.

On 10 *April* a Symposium and discussion were held jointly with the Systematics Association on 'Infra-specific variation in relation to ecology'. The meeting was under the chairmanship of Dr J. W. Gregor. The first paper was given by Dr J. Heslop-Harrison on 'Ecological polymorphism in orchids'. He pointed out that there has been very general acceptance of Turesson's view of the ecotype as '...the product arising as a result of the genotypical response of a species to a particular habitat'. Broadly, the argument is that adaptation to the varying habitats encountered by a species in the course of migration takes place through the selective elimination of unfitted biotypes, the ecotypes being the outcome of this selection. A plausible corollary of this is that phenotypically similar ecotypes might arise in spatially separate but ecologically similar habitats, where like selective forces have been at work on the species. Turesson did, indeed, himself produce evidence that this was likely to be so in species such as *Hieracium umbellatum*. It is possible, however, that the ecologically correlated polytypy shown by some species has not arisen as a direct response to *local* habitat conditions at all, but through the independent migration of several ecological races all originally allopatric. A species which possibly provides an example of this is '*Orchis latifolia* L. sec. Pugsl. (=*O. strictifolia* Opiz, *O. incarnata* auct. mult.)'. The taxonomic species is here fairly well defined by a number of morphological characteristics, but within its limits there is a considerable amount of variation, a large part of which concerns flower colour, pattern and shape. Study of populations of the species in various parts of the British Isles has shown that some aspects of the floral variation are correlated strongly with habitat type. Forms corresponding broadly with the taxonomic varieties *coccinea*, *ochroleuca*, *pulchella* etc., are sufficiently characteristic of certain types of habitat to merit description as 'ecotypes', if the correlation of 'plant type' with 'habitat type' is the sole criterion employed. The designation of 'ecotype' has in fact been applied to the var. *serotina*, a form characteristic of *Sphagnum* bogs. It is, however, difficult to see how local selection can have produced populations of practically identical facies in so many widely scattered localities, particularly when in many of these there is no 'hinterland' of an undifferentiated species population, and when the phenotypic characters mostly concerned are floral ones. The alternative explanation is that the vars. *ochroleuca*, *coccinea*, etc. represent ecological races of the species, differentiated perhaps in former isolation, which have gained their present distributions by migration independently of each other. A possible interpretation of the significance of the differences in floral features emerges here, since it may be that these have provided an ethological isolating mechanism which has permitted the different races to retain their genetic integrity during the period of migration, when reproductive contacts with others may otherwise have disrupted their particular adaptive gene complexes. Observation of bee behaviour in polymorphic colonies would be desirable to establish this point.

Prof. Valentine in the discussion pointed out that the fen form was presumably a different ecotype, with a superimposition of flower differentiation. He also stressed that isolation between the various forms may exist in nature but they intercross under cultivation in the greenhouse.

Dr Gregor stressed the importance of sympatric differentiation. While Dr Riley discussed the possible significance of the seed dispersal in the spread of certain biotypes, Dr Hope-Simpson suggested the heterotopic origin of flower colour with subsequent differentiation in relation to habitat. Dr Heslop-Harrison agreed that it was probably of heterotopic origin.

Dr H. G. Baker then gave an account of ecotypical variation in the closely related species *Geranium*

purpureum Vill. and *G. robertianum* L. Both species are almost habitually self-pollinated, consequently populations tend towards homozygosity and to the production of clearly recognizable biotypes, whilst differences are often between populations rather than between individuals.

British material of the annual *G. purpureum* contains a rock-form with strictly upright growth and a prostrate maritime form which retain their distinctive characters in cultivation. When grown in Leeds, however, abnormalities and poor seed-setting are evident while the plants are not frost-hardy, which may be correlated with the Mediterranean affinities of the species.

In *G. robertianum*, prostrate maritime races and an ascending woodland (and scree) race are distinguishable. Many characters used by the authors of varieties, etc., have been shown to be direct effects of the environment while each race contains a complete cline from glabrous to densely hairy populations. Thus the ecological grouping within the species tends to cut across the morphological treatments. The subspecies *celticum* is a race with specialized climatic and edaphic requirements found only in open situations on limestone in the west of the British Isles. Native North American material also consists of a series of races, some prostrate, others upright.

All races of *G. robertianum* are tetraploid ($2n=64$) and are fully interfertile. *G. purpureum* is diploid ($2n=32$) and artificial interspecific hybrids are nearly sterile triploids. Nevertheless, complete fertility is recovered by some plants in the F_3 generation. Consequently, *G. robertianum* and *G. purpureum* represent separate ecospecies of the same coenospecies.

Studies of this kind are of direct importance to the ecologist for they give a closer picture of the species as an indicator of environmental conditions.

Preliminary observations upon two other genera were also reported. In *Picris echioides* a race from the sea-cliffs east of Brighton is perennial, self-incompatible, late-flowering and decumbent, while a race in culture from the margin of an arable field near Clayton, Sussex, is annual or biennial, self-compatible, relatively early flowering and possesses an upright habit. The characters of the latter were interpreted as adaptations to life as a weed of arable land.

In *Adoxa moschatellina*, plants collected in 1952 from a cleft in limestone rocks at *c.* 2100 ft. on Ingleborough, Yorks, were found to be later leafing and flowering (whilst in culture) than some lowland, woodland plants. There appears to be a similar disjunction between montane and woodland plants in some of the Scottish mountain regions and an appeal was made for the collection of material for cultivation to determine whether ecotypical variation occurs in a species which appears to have run out of morphological variation. (*Adoxa moschatellina* has no known varieties and is the only known species of the only genus in the isolated Adoxaceae.)

The discussion that followed dealt primarily with the differentiation of coastal forms of species, and with the disjunction that often exists between them and inland forms. The possible physiological and genetical difference between them was also discussed, and the part played by this form of ecological isolation in the development of subspecific units. Drs Gregor, Heslop-Harrison, Walters and Gorham took part in this discussion.

Dealing with 'Plant variation and habitat on Chalk Downs', Dr J. F. Hope-Simpson presented some of the results of transplant experiments conducted at Oxford in 1938–40. The purpose was to supplement earlier genecological work, primarily concerned with wide habitat range, by examination of population differences between habitats not showing such wide disparity and sometimes very close together. All the habitats were in chalk grassland. Pairs in close proximity, illustrated by lantern slides, were represented by the opposing sides of a steep coombe and by biotic ecotones (quoted below for *Festuca rubra* and *Poterium*). Although the habitat samples had to be small (20 minimal rootings being taken per habitat) a watch was kept on non-genetic variability in the experimental garden by growing sets of clones. Diagrams and photographs showed conclusive results, after 2 years' garden growth, in *Festuca ovina*, *F. rubra* and *Poterium sanguisorba*. In *Festuca ovina*, tussock spread was greater in plants of north-aspect than of nearby south-aspect origin. In *F. rubra*, florifery as seen in culture showed an inverse relation to the depth of the original herbage, the latter being represented diagrammatically as the resultant of grazing intensity plus dampness or dryness. Two well-differentiated populations were only a few metres apart, with an old rabbit-proof fence between. *Poterium sanguisorba* showed differentiation in tussock-spread and height, as between samples from populations about 35 m. apart, the smaller plants being

from grazed turf with very abundant *Poterium*, and the larger from dense *Brachypodium pinnatum* which had invaded it and reduced the *Poterium* to occasional plants. Natural selection had evidently occurred for a property, competitive vigour, which showed in the garden as spread and height. Dr Hope-Simpson emphasized that differences displayed in culture would not necessarily be manifested in the same way in the original habitat: a power of copious florifery, for instance, might or might not be important as such in closely cropped turf. It was important to bear this in mind when regarding genotypic uniformity (as judged in the garden against clonal uniformity) in a given attribute as a sign of its selective value in the particular habitat.

This account terminated the morning session.

The afternoon session was opened by Miss Patricia J. Watson who read a paper on the 'Distribution in Britain of chromosome races of *Festuca ovina*'.

It has been known for some time that two chromosome numbers occur within *F. ovina sensu ampliss.* in the British Isles and it has been suggested that the diploid might be identified as *F. tenuifolia* Sibth., the tetraploid as *F. ovina* L. Unfortunately, it has been found impossible to distinguish between the diploid and the tetraploid in the wild since the only point of distinction between the two species which is unaffected by environment is the presence or absence of an awn on the flowering glume and in this as in all other characters, the two chromosome races show a considerable overlap in their ranges. This was confirmed by a replicated trial grown in the uniform environment of an experimental garden with plants grown from seed collected from diploid and tetraploid populations grown in isolation. It was found that the mean for the diploids differed statistically from the mean for the tetraploids but that the overlap of values was considerable. Many random collections from populations all over the British Isles were made and chromosome counts taken from root tips. It was found that there is a definite pattern of distribution with the diploid occurring in Scotland north of the Lowlands and on the East coasts of Scotland and England, at least as far south as the Cleveland Hills, with, at present, a single occurrence in the Breckland area near Cambridge. The tetraploid occurs exclusively in Wales, Ireland, south and west England, south-west Scotland with a curious projection in the centre of Scotland almost reaching Inverness. In the south-east of Scotland and north-east of England several populations were collected which contained both diploid and tetraploid plants. The presence of diploids in the dry, sandy area of the Breckland suggests that a further detailed investigation, which is to be undertaken, of the pH tolerance of the two chromosome races may yield interesting information. So far only one tetraploid which could be attributed to one of these two species has been reported from the Continent, namely from France. All material obtained from seed from the Scandinavian countries, Holland and France has proved to be diploid so it would seem possible that the tetraploid has arisen within Great Britain, probably in the south of England. The viviparous form which occurs exclusively in wet, mountain areas and in the islands of Scotland is tetraploid with the exception of two triploid populations.

Following this account a discussion took place of Dr Hope-Simpson's paper. The importance of whether the plants selected for transplantation to the experimental garden were vegetative or flowering was stressed by Dr Gregor and Dr Gorham. Dr Hope-Simpson replied that the forms were mostly flowering and that those from heavily grazed areas had in the experimental garden smaller tillers and a higher degree of florifery.

Miss Watson's paper was then discussed. In reply to Prof. Valentine, it was stated that the area covered by the populations in the field was about the size of the lecture room. Prof. Valentine also stressed the importance of defining exactly the habitat of the diploid fescue in Breckland. In reply to Dr Gorham Miss Watson stated that the Breckland *Festuca ovina* came from a closed sward. Dr Riley suggested the autopolyploid origin of the tetraploid but Miss Watson indicated that no success had been obtained by the use of colchicine.

The final paper of the meeting was given by Dr R. Riley on 'Ecotypes of *Thlaspi alpestre*'.

Samples from a single population of *Thlaspi alpestre* at Llanrwst, Matlock and Malham, and from a number of populations around the Tees-South Tyne watershed were grown from seed in a uniform plot.

Populations on the Teesdale side of the Tees-South Tyne watershed differed from those of the South Tyne side in a number of quantitative characters, although they occurred in the field in areas with similar environmental conditions. The causes of the origin of genetic differences between populations were

discussed. It was suggested, on the evidence of clinal variations, which was not accompanied by a gradation in environmental conditions, that in this case gene migration might be important from a population, on the Tees, at an altitude 900 ft. below that of the watershed populations.

There was considerable variation in habit, and when plants were classified into arbitrary habit categories differences in frequencies were shown between populations. In the higher altitude populations forms with extremely short stems, that carried the inflorescence scarcely clear of the tussock, were most frequent. At lower altitudes the plants were taller and the inflorescences were borne well clear of the tussock. Such plants had habits varying from erect to decumbent, and the erect forms were more frequent where grazing was least. Thus at higher altitudes, the dwarf habit is more frequent due to the selection effect of climatic exposure, and grazing is not important in selection, and only becomes so at lower altitudes where the plants are taller. The relative importance of these two ecological factors in the occurrence of populations of *T. alpestre* characterized by a predominance of any particular habit form is such that grazing only becomes important when the selection pressure exerted by climatic exposure is relaxed.

In the discussion that followed there was some speculation as to the original habitat of *T. alpestre*. Dr Riley stressed the importance of light, and that competition played little part where it occurred. In reply to Dr Baker, Dr Riley said that no microscopic remains of *T. alpestre* had been found in peat deposits. Professor Valentine and Dr Heslop-Harrison took part in this discussion. Clinal variation was referred to by Dr Gregor and Dr Baker—who stressed that in other species (such as *Achillea* in California) clinal variation in relation to environment did occur.

Dr Gorham suggested that the difference in the lead content of the soil might influence its uptake by the plant. Professor Clapham pointed out that there was no dependence on lead by the plant.

A more general and lengthy discussion followed, the nature of which precludes a detailed report. The main lines of discussion are however outlined. Dr A. S. Thomas mentioned ecotypic differentiation in the coffee tree, where variation in flowering in relation to latitude was found. Dr Gregor went on to stress the importance of clinal variation in characters in relation to ecological factors. Where such variation existed the term ecotype was not applicable. Dr Gregor quoted an existence of dark mice in New Mexico, where gene flow occurred from an adjacent habitat with white mice. This was evidence against the use of the term ecotype. Dr Baker, referring to his work on *Melandrium*, stressed the significance of geographical isolation in the development of sub-specific variation and speciation generally—then the relinking of species with sub-units and ensuing hybridization. He also referred to the existence of clines (hairiness) in *Geranium robertianum* which had no ecological significance.

Dr Heslop-Harrison stressed the importance of glacial survival in the case of some species in interpreting the origin of infra specific variants.

Dr R. E. Hughes called attention to the possible use of Fisher's discriminant function and certain adaptions of it in sub-specific classification. Dr Heslop-Harrison mentioned the mathematical difficulties which at the moment precluded the use of this function.

Others who took part in the discussion were Dr Hope-Simpson, Dr Burtt and Prof. Valentine.

This meeting with the Systematics Association proved a very useful review of work in progress on infra-specific variation in relation to various environmental factors.

On the evening of 10 April, the Botanical Society of Edinburgh invited the Society to a soirée at the Royal Botanic Garden. The soireé was very well attended by members of the Botanical Society of Edinburgh, the Systematics Association and the British Ecological Society, about 110 persons being present. Numerous exhibits were put up by members of these Societies, the UniversityBotanyDepartment and the Royal Botanic Garden, Edinburgh. The evening was very successful and enjoyable. Professor Valentine expressed the thanks of the visiting Societies to the Botanic Society of Edinburgh for arranging the soirée and for the hospitality and the very excellent refreshments provided.

On the morning of 11 April the Systematics Association held a discussion on 'Taxonomic research—the problems and methods respectively suitable to the Universities and major Herbaria'. Several members of the British Ecological Society were present.

Dr R. D. Meikle, Hon. Secretary of the Systematics Association, reports as follows for the information of members of the British Ecological Society:

'The nature of the discussion precluded a detailed report, but the following resolutions, passed at the meeting, were referred to the Systematics Association Council for consideration.

'(1) That the Council should contact the Universities with a view to obtaining a list of unpublished papers and theses on subjects of interest to systematists. It was felt that a great deal of interesting and valuable matter was being disregarded because of the present inaccessibility of such papers and theses.

'(2) That the card-index of taxonomic research kept by Mr B. C. Burtt and the Botanical Secretary should be revised and published.

'(3) That the Association should be represented at the next International Botanical Congress (to be held in Paris, 1954) and that a discussion should be arranged on "The Progress of Work on the European Flora".

'The Council has considered these resolutions and a report on action taken will be given later.'

R.E.H.

SUMMER MEETING AT MALHAM TARN

The Summer Meeting was held at the Malham Tarn Field Centre from 1 to 6 July, by kind permission of the Council for the Promotion of Field Studies and the Warden, Mr P. F. Holmes. About thirty members arrived on the afternoon of Wednesday, 1 July, and, after dinner, heard an interesting and informative talk from the Warden on the geology and topography of the Craven Pennines. On the following day Mr Charles Sinker led the party on a walk over grassland and limestone pavement and showed evidence for his view that most of the pavement now bare was formerly drift-covered, and that removal of the drift is still in progress. Striae and large numbers of transported boulders, including many of Millstone Grit, showed that ice had passed over the pavement, and in some localities there was a considerable depth of yellowish non-calcareous loamy drift overlying pavement. This could readily be identified by the prominence of *Nardus* and *Galium hercynicum*, contrasting with the limestone-grassland vegetation of the surrounding slopes and the calcicole species of the bare pavement. Mr Sinker suggested that climatic conditions in the Craven Pennines after the retreat of the ice had always favoured the gradual transport of drift-particles into the progressively widening and deepening fissures, or grikes, of the underlying pavement. Where the drift-cover was originally thin its complete removal may have antedated the forest-period. Where it was thicker, and persisted until forests developed, its final removal may have been delayed until post-Neolithic deforestation expedited the process again. Of special relevance was an Iron Age cattle enclosure, identified by Dr A. Raistrick and demonstrated to the party by him. Its still recognizable walls enclose what is now almost completely bare pavement, but what must surely have been grass-covered drift at the time of use.

An interesting area of partially concealed pavement occasioned some dispute as to the status of small plants of *Calluna*, whether relict in an area almost denuded of drift or invading at a stage in soil formation on bare pavement. Subsequent pH determinations suggest that here both upgrade and downgrade processes may be at work, colonization of bared limestone by mosses leading to the accumulation of a black organic 'soil', later colonizable by *Festuca ovina* and associated species and eventually by *Calluna*.

The pavement examined before lunch lay chiefly to the north of the Tarn House. After lunch the party proceeded along the east side of the Tarn to examine first the aquatic vegetation of an outlet stream and then the curious large hummocks in an area of grassland over Silurian shales. No wholly convincing explanation of these hummocks could be offered, and the party proceeded along a dry limestone valley to the impressive area of pavement above Malham Cove. Here, in grikes much deeper than had been seen previously, a typical pavement flora was examined. The most abundant species were *Geranium robertianum*, *Mycelis* (*Lactuca*) *muralis*, *Mercurialis perennis*, *Epilobium montanum*, and the ferns *Phyllitis scolopendrium*, *Asplenium ruta-muraria*, *A. trichomanes* and *A. viride*. *Actaea spicata* was seen locally, and it was noted that *Phyllitis*, *Oxalis acetosella* and *Geranium robertianum* were the vascular plants extending to the greatest depths in narrow grikes. Shallow, well-lighted grikes were commonly dominated by *Sesleria caerulae*. Bryophytes were prominent, especially in grikes of intermediate size and depth.

The day's excursion ended with a visit to Malham Cove, where *Polemonium caeruleum* was at the height of its flowering.

Fig. 1. Profile transect of a belt 30 ft. wide.

COLT PARK WOOD

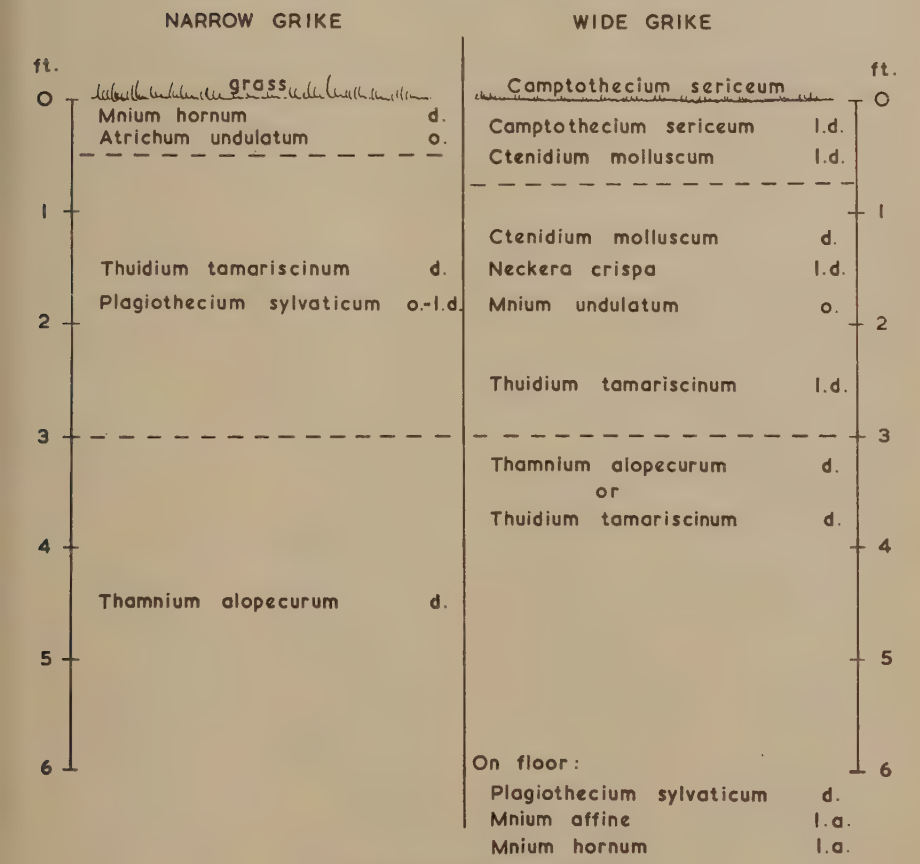

Fig. 2. Moss zonation in grikes.

On Friday, 3 July, there was an excursion to Moughton Fell under the leadership of the veteran Yorkshire naturalist, Mr Chris Cheetham, assisted by Mr Sinker. The party assembled at the south-east corner of the hill and first inspected the exposure of up-ended Silurian slates upon which the base of the Carboniferous Limestone rests unconformably. The route then led to Long Scar and the excellent limestone pavement above it. The most abundant plants of the Scar were *Sesleria caerulea*, *Scabiosa columbaria* (some of it pink-flowered) and *Mycelis* (*Lactuca*) *muralis*, and *Silene maritima*, *Sedum acre*, *Lotus corniculatus*, *Thymus drucei* and *Galium pumilum* were frequent. Moughton differs from the higher Craven hills in having no cap of Millstone Grit, but Grit erratics, probably from Ingleborough, were seen in abundance. The extensive and well-developed pavements were remarkable chiefly for the rich fern flora, which included the local *Dryopteris villarsii* and a large amount of *Thelypteris robertiana*. Overlooking the valley separating Moughton from the hill to its west was a coarse scree-slope at about 1225 ft. Here an open community with *Festuca ovina*, *Sesleria caerulea* and *Linum catharticum* as the most abundant species and with frequent *Thymus drucei*, *Campanula rotundifolia*, *Galium pumilum*, *Briza media* and *Viola riviniana* ssp. *minor*, included small patches of *Saxifraga oppositifolia*, a further relict plant of great interest. Some time was then spent in examining one of the valley-heads dominated by *Juniperus communis*, a special feature of Moughton, and a search for *Listera cordata* was rewarded by the discovery of a plant in the mossy Callunetum associated with the junipers. The day was a most enjoyable one, and the Society's best thanks are due to Mr Cheetham whose robust personality and intimate knowledge of the hill added greatly to the pleasure and profit of the excursion.

On Saturday, 4 July, visits were paid to two areas of ancient woodland near the north-eastern corner of Ingleborough. The first was Colt Park Wood, where members of the party made systematic observations on the composition and structure of this most interesting but scantily studied fragment of ashwood on limestone pavement at 1125 ft. above sea-level. Examination was restricted to the northern end of the wood, where trees are more numerous than towards the southern end. The pavement here has grikes varying greatly in width (6 in. to 8 ft.) and in depth (1·5 to 10 ft.). Trees of *Fraxinus excelsior*, from 25 to 40 ft. in height, dominated the vegetation. Most were growing in grikes, but some were set on clints with

	Grikes	Clints		Grikes	Clints
Actaea spicata	r.	—	G. urbanum	r.	r.
Adoxa moschatellina	r.	—	Heracleum sphondylium	o.	—
Allium ursinum	o.	—	Luzula sylvatica	r.	—
Anthoxanthum odoratum	—	o.	Melandrium rubrum	f.	r.
Arabis hirsuta	r.	—	Mercurialis perennis	l.a.	r.
Arctium nemorosum	—	r.	Milium effusum	r.	—
Arrhenatherum elatius	f.	f.	Moehringia trinervia	l.	—
Asperula odorata	r.	o. (sides)	Mycelis muralis	o.	—
Campanula latifolia	f.	r.	Myosotis arvensis	r.	f.
Cardamine flexuosa	—	r.	Orchis mascula	—	vr.
Chamaenerion angustifolium	*r.	—	Oxalis acetosella	o.	—
Chrysosplenium alternifolium	vr.	—	Paris quadrifolia	vr.	—
C. oppositifolium	r.	—	Poa pratensis	—	r.
Circaea lutetiana	o.	—	P. trivialis	f.	f.
Conopodium denudatum	r.	—	Primula vulgaris	r.	—
Crepis mollis	v.r.	—	Prunus padus *seedlings*	r.	—
C. paludosa	o.	—	Rubus idaeus	o.	—
Dactylis glomerata	—	o.	Saxifraga hypnoides		r.
Endymion non-scriptus	o.	—	Senecio jacobaea	r.	r.
Epilobium montanum	f.	o.	Sesleria caerulea	—	r.
Festuca ovina	—	r.	Sorbus aucuparia *seedlings*	—	r.
F. rubra	—	f.	Stachys sylvatica	r.	—
Filipendula ulmaria	o.	—	Stellaria holostea	—	o.
Fragaria vesca	—	o.	Succisa pratensis	r.	—
Fraxinus excelsior *seedlings*	r.	v.r.	Taraxacum officinale	—	r.
Galium aparine	r.	—	Urtica dioica	f.	f.
G. cruciata	—	r.	Valeriana officinalis	o.	—
G. pumilum	—	r.	Veronica chamaedrys	f.	f.
Geranium lucidum	o. (sides)	r.	Vicia sepium	—	r.
G. robertianum	f.	f.	Viola lepida	—	o.
G. sylvaticum	o.	—	V. riviniana	r.	r.
Geum rivale	r.	r.			

* Rooted in bark of dead *Fraxinus*.

roots extending down into adjacent grikes. Their short trunks were thickly covered with *Hypnum cupressiforme* and lichens. *Prunus padus*, 7–15 ft. high, rooted in grikes, was abundant in a shrub-layer beneath the ash, with *Betula pubescens*, *Sorbus aucuparia*, *Corylus avellana*, *Viburnum opulus* and *Acer pseudoplatanus* less frequent. Counts within a sample area of the closed wood gave *Fraxinus* 48, *Sorbus* 28, *Prunus padus* 48 (+2 marginal thickets), *Crataegus* 5, *Sambucus* 2, *Viburnum opulus* 1, *Corylus* 1, *Acer pseudoplatanus* 1. Some young seedlings of *Fraxinus*, *Prunus* and *Sorbus* were observed, but it was clear that sheep-grazing was militating strongly against successful regeneration.

The table on p. 576 shows the list of flowering plants observed in the more or less closed ashwood.

The following ferns were noted:

Asplenium ruta-muraria: rare, in fissures near the top of an irregularly weathered rock.

A. trichomanes: occasional: confined to the sides of grikes, just below pavement-level.

Cystopteris fragilis: occasional in fissures on the sides of grikes, but extending no more than 2 ft. below pavement-level.

Dryopteris austriaca (*dilatata*): chiefly epiphytic on the mossy bases of *Fraxinus* at pavement-level, but also in black organic soil on the floor of wide grikes.

Dryopterus filix-mas: the most abundant fern in the interior of the wood, and locally very abundant in wide grikes.

Phyllitis scolopendrium: frequent at all levels on the sides and floors of grikes.

Polystichum lobatum: very rare, in deep grikes.

Polypodium vulgare: rare as an epiphyte on the bases of *Fraxinus*.

Pteridium aquilinum: chiefly marginal (see below).

The only bryophytes playing a significant part in the colonization of bare clints were *Grimmia apocarpa*, in small tufts, and the mat-forming species *Hypnum cupressiforme*, *Ctenidium molluscum* and *Camptothecium sericeum*. It was evident from this visit during a hot dry spell that these clint-colonizing mosses readily became detached from the rock when desiccated.

The walls of grikes carried a much richer and more luxuriant bryophytic flora, and the accompanying diagrams give examples of the types of zonation observed. Trunks of *Fraxinus* and *Prunus padus* commonly carried *Mnium hornum* and *Dicranum scoparium* up to about 2 ft. from the base and *Hypnum cupressiforme* var. *filiforme* from this point upwards to as much as 12 feet from the base.

On the western margin of the wood there was an area with stiff reddish drift covering the pavement to varying depths, though bare clints emerged here and there. The canopy here was much interrupted and *Pteridium aquilinum* was generally dominant with *Holcus lanatus* locally dominant and with *Arrhenatherum elatius* and *Mercurialis perennis* locally abundant. Many tall-growing grasses and herbs were associated especially with the *Holcus*, these including *Dactylis glomerata*, *Deschampsia caespitosa*, *Festuca rubra*, *Campanula latifolia*, *Centaurea nigra*, *Cirsium heterophyllum*, *C. vulgare*, *Filipendula ulmaria*, *Geranium sylvaticum*, *Heracleum sphondylium*, *Melandrium rubrum* and *Rubus idaeus*. There was also much *Geranium robertianum*, *Asperula odorata*, *Convallaria majalis* and *Veronica chamaedrys* on clints or in grikes in this area.

Adjoining this drift-covered area on the western margin of the wood was a flush with black peaty soil. From this the following list was made:

Allium ursinum	o.	Mercurialis perennis	l.d.
Campanula latifolia	f.	Poa trivialis	o.
Cirsium heterophyllum	a.	Prunus padus	o.
Crepis paludosa	r.	Pteridium aquilinum	f.
Dryopteris filix-mas	o.	Ranunculus repens	l.d.
Filipendula ulmaria	o.	Sambucus nigra	v.r.
Fraxinus excelsior	r.	Senecio jacobaea	o.
Geum rivale	o.	Urtica dioica	o.
Holcus lanatus	l.a.	Veronica chamaedrys	f.
Melandrium rubrum	o.		

In the afternoon the party crossed the Ribble at a point close to Colt Park Wood and proceeded to Ling Ghyll, where the Cam Beck flows through a wooded limestone gorge. A halt was made in order to examine the luxuriant vegetation near the downstream end of the wood where the canopy was com-

posed of *Ulmus glabra*, *Fraxinus excelsior* and *Sorbus aucuparia*, with *Prunus padus* and a little *Corylus avellana* as associated shrubs. Trees of *Acer pseudoplatanus* were nearby. The accompanying table shows species observed along a transect across the valley.

	A	B	C	D	E
Acer pseudoplatanus *seedlings*	—	—	—	o.	—
Agropyron canium	—	—	—	—	r.
Ajuga reptans	—	r.	—	—	—
Alchemilla glabra	r.	—	—	—	—
A. xanthochlora	r.	—	—	—	—
Allium ursinum	o.	—	o.	—	l.f.
Angelica sylvestris	—	—	r.	—	—
Anthoxanthum odoratum	—	—	—	—	o.
Arctium nemorosum	—	—	—	—	r.
Arrhenatherum elatius	—	r.	—	o.*	l.a.
Asperula odorata	—	—	o.	o.	—
Asplenium trichomanes	—	l.	—	o.	—
Athyrium filix-femina	l.a.	—	—	—	—
Bellis perennis	—	—	—	—	r.
Brachypodium sylvaticum	l.a.	—	o.	—	f.
Bromus ramosus	—	—	—	—	o.
Caltha palustris	—	—	o.	—	—
Campanula latifolia	—	—	r.	—	r.
C. rotundifolia	—	—	—	o.	—
Cardamine flexuosa	—	—	o.	—	—
Centaurea nigra	—	—	—	—	o.
Chrysosplenium oppositifolium	—	—	l.	—	—
Circaea lutetiana	—	—	o.	—	—
Cirsium heterophyllum	—	—	—	—	l.f.
Conopodium denudatum	—	—	r.	—	o.
Crepis paludosa	r.	—	o.	—	—
Cystopteris fragilis	—	l.f.	—	o.-l.f.	—
Dactylis glomerata	r.	—	—	—	l.a.
Deschampsia caespitosa	l.	—	—	—	—
Dryopteris austriaca	o.	—	o.	—	—
D. filix-mas	o.	—	—	—	o.
Epilobium montanum	r.	—	—	o.	o.
Festuca gigantea	—	—	r.	o.*	—
F. ovina	—	—	—	o.*	—
F. rubra	—	—	—	—	l.f.
Filipendula ulmaria	r.	—	o.	—	l.f.
Fragaria vesca	o.	—	—	—	o.
Fraxinus excelsior *seedlings*	—	—	—	o.	—
Galium cruciata	—	—	r.	—	f.
Geranium robertianum	f.	—	o.	f.	f.
Geum rivale	r.	—	—	—	—
G. urbanum	o.	—	—	—	—
Helictotrichon pratense	—	—	—	—	o.
Heracleum sphondylium	—	—	r.	—	—
Holcus lanatus	—	—	—	—	f.

	A	B	C	D	E
Hypericum hirsutum	—	—	—	—	r.
H. pulchrum	—	r.	—	—	—
Lonicera periclymenum	—	l.	—	—	—
Melandrium rubrum	r.	—	—	—	l.f.
Melica nutans	—	—	—	o.*	—
M. uniflora	—	—	o.	—	—
Mercurialis perennis	f.-l.a.	—	l.a.	f.	l.a.
Moerhringia trinervia	r.	—	—	—	—
Mycelis muralis	—	—	—	o.	l.a.
Myosotis arvensis	—	—	r.	r.	o.
Oxalis acetosella	o.	—	—	o.	o.
Phyllitis scolopendrium	—	—	—	o.	—
Poa pratensis	—	—	—	—	o.
P. trivialis	l.f.	—	—	—	—
Polypodium vulgare	—	—	—	r.	r.
Polystichum lobatum	—	r.	—	—	—
Primula vulgaris	r.	—	—	—	o.
Prunella vulgaris	r.	—	—	—	—
Ranunculus acris	—	—	—	—	o.
Rubus idaeus	l.	—	—	—	—
Sanicula europaea	a.-l.d.	—	o.	—	—
Scrophularia nodosa	r.	—	—	—	—
Senecio jacobaea	r.	—	—	—	—
Stachys sylvatica	r.	—	—	—	l.f.
Stellaria holostea	—	—	—	—	o.
Succisa pratensis	r.	—	—	—	—
Taraxacum officinale	—	—	—	—	o.
Trisetum flavescens	—	—	—	—	r.
Urtica dioica	l.	—	o.	—	—
Valeriana dioica	r.	—	—	—	—
V. officinalis	l.f.	—	—	—	o.
Veronica chamaedrys	r.	—	—	—	o.
V. montana	r.	—	r.	—	o.
Vicia sepium	—	—	—	—	l.
Viola riviniana	—	—	—	—	o.
Conocephalum conicum	l.	—	—	—	—
Ctenidium molluscum	—	l.a.	—	—	—
Mnium punctatum	l.	—	—	—	—
M. undulatum	—	—	—	—	—
Neckera crispa	—	l.a.	—	—	—
Pellia epiphylla	l.	—	—	—	—
Rhytidiadelphus squarrosus	—	—	—	—	o.
Thamnium alopecurum	—	l.	f.	—	—
Tortella tortuosa	—	l.a.	—	—	—

* on well-marked ledges.

A. Steep earthy slope, about 5 ft. high, forming north-west-facing bank of stream.
B. Rock-wall above A.
C. Boulders and shingle by the stream at foot of south-east-facing cliff.
D. Cliff forming south-east-facing side of valley.
E. Broad grassy sloping ledges above D.

On Sunday, 5 July, visits were made to Malham Tarn Moss and Great Close Mire, both within easy distance of the Field Centre. The Moss was approached from the north side. Mr Sinker halting the party at a point on the Tarn margin between the Tarn House and the inflow stream passing along the north side of the Moss, where, in a small sheltered bay, there was reed-swamp dominated by *Carex rostrata*. After examining sedge-fen in which *C. rostrata*, *C. diandra*, *C. approprinquata*, *C. disticha* and *C. nigra* (in a curious tussocky form) varied in abundance with variations in the level of the peat-surface, a route was followed that led through willow carr, with a bewildering mixture of species and hybrids, to the margin of the Moss. Here it was explained that the Tarn and the Moss together occupy a basin-shaped

depression walled by limestone slopes and scars except on the southern side where water was earlier held up by ridges of outwash sands and gravels, its only outlet being through Great Close Mire to the east and down into Gordale Beck. Later the outwash ridges were breached at the present Water Sinks valley, so that the Tarn and Great Close Mire became permanently separated. It was presumably after this that continuous accumulation of organic and inorganic deposits in the western half of the Tarn basin led to the raising of its floor to the point at which vegetation could establish itself, a *Carex* swamp being succeeded first by birch and willow carr and then by *Sphagnum* bog. Deep borings in the centre of the Moss have revealed lowermost clays, sandy layers and marls probably referable to the Late Glacial period, then detritus-muds laid down in fairly deep water, and finally the succession of peat-layers in which the remains of sedge-swamp, fen-carr and bog plants are readily recognizable in ascending sequence. The total depth to the gravelly floor reaches about 10 metres, of which more than 6 metres represents bog-peat.

Upward growth of the bog has been checked by draining and burning at intervals during the past century or two, and further changes were brought about by the raising of the water-level in the Tarn by about 4 ft. in the middle of last century. This rise in level has caused considerable erosion of the bog-margin on the side adjoining the Tarn and has also led to an extension of fen vegetation, alongside the inflow streams. The present marginal fen must therefore not be regarded as natural 'lagg' communities, though vegetation of a similar kind may always have been present but on a much less extensive scale.

Before leaving the Moss the party examined a patch of *Andromeda polifolia* and pools containing *Cinclidium stygium*. After lunch they walked eastwards to the other part of the original lake basin, that now occupied by Great Close Mire. This is a large area through which seepage water makes its way in numbers of anastomozing streamlets whose beds are covered with calcareous tufa. Mounds of surface-leached calcareous drift carry calcifuge vegetation on their tops and such moisture-loving calcicoles as *Primula farinosa*, *Pinguicula vulgaris* and *Carex hostiana* on their sides. As occasional associates of these calcicoles *Bartsia alpina*, *Polygala amarella* and *Carex capillaris* were demonstrated by Mr Sinker. The most frequent species of the tufa-covered lows between the mounds were *Carex lepidocarpa*, *C. panicea* and various calcicole mosses. It was evident that cattle now played an important part in preventing effective colonization of the 'lows', but it was agreed that the habitats for the relict calcicoles may always have been maintained, though on a smaller scale, by water-erosion.

This concluded a most enjoyable meeting held in superb weather. The best thanks of the Society are due to Mr Paul Holmes and Mr Charles Sinker for their organization of the excursions and for giving so much time and trouble to make members comfortable in the Tarn House.

A.R.C.

THE ANNUAL GENERAL MEETING

6 January 1954

By courtesy of Prof. A. R. Clapham the Annual General Meeting was held in the Department of Botany, The University, Sheffield. Accommodation was provided at Crewe Hall. Members were entertained at a Soirée at Crewe Hall at 8 p.m. on the evening of 5 January. A range of exhibits was available illustrating ecological work in progress at the Department of Botany at Sheffield. Excellent refreshments were provided, and there was ample opportunity for discussion. The Society is indebted to Professor Clapham for the arrangements made and the enjoyable evening.

The Annual General Meeting, 6 *January*, started at 10 a.m. Thirty-five members of the Society were present. In the absence of the President, Dr C. B. Williams, Dr A. S. Watt took the Chair. The minutes of the last Annual General Meeting were read by the Honorary Secretary, Dr R. E. Hughes. On the motion of the Chairman, these were accepted by the Society and signed by him. Then followed the annual report of the Honorary Secretaries which was again read by Dr R. E. Hughes.

Minutes of the Annual General Meeting, 6 January 1953

The Annual General Meeting on 6 January 1953 was held at the Department of Botany, University College, Gower Street, London, by courtesy of Prof. W. H. Pearsall. The President of the Society, Dr C. B. Williams, was in the chair. Over 100 members were present.

The Honorary Secretary read the Minutes of the Annual General Meeting of 1952. These were accepted and signed by the President. The Annual reports of the Honorary Secretaries and Treasurers were then given. On the motion of the President the Treasurers' report was accepted.

The president then proposed and the Society agreed to the renewal of the following grants: The Freshwater Biological Association £10; The Co-ordinating Committee for Nature Conservation £2. 2*s*. 0*d*.

On the proposal of Dr H. Godwin, Messrs William Norman and Sons were re-elected Auditors of the Society.

The Honorary Editors then gave their reports.

(*a*) *Journal of Ecology*. Dr Godwin referred to the appointment of Dr D. E. Coombe to be Honorary Assistant Editor. It was reported that there was no lack of material for publication. Its standard was satisfactory, but contributions should be briefer. The expense of publishing the coloured plates which had recently appeared in the *Journal* was not borne by the Society. During the year there were two more contributions to the Biological Flora (T. E. T. Bond, *Elymus arenarius*; Howard and Lyon, *Nasturtium officinale* R.Br., *N. microphyllum* Boenningh ex Rchb.).

(*b*) *Journal of Animal Ecology*. Mr Gilson mentioned the change in the form of the *Journal*. Abstracts of publications on animal ecology would be resumed in 1953, these being edited by Prof. L. A. Harvey, while Mr R. S. R. Fitter was responsible for the abstracts of papers from local Natural History Societies. Some modification would be made in the grouping of the material.

Both reports were accepted by the Society.

Mr Gilson then proposed that £20 be paid to Dr Hobby for checking the bibliographies in the *Journal of Animal Ecology*. This was agreed to.

The Society then proceeded to the election of members of the Council and its officers. On the proposal of the President the following were elected:

President: C. B. Williams.
Vice-Presidents: W. B. Turrill (1 year), J. A. Kitching.
Hon. Secretaries: G. C. Varley, R. E. Hughes.
Hon. Treasurers: V. S. Summerhayes, C. E. Hubbard.
Hon. Editors: H. Godwin, H. C. Gilson.
Hon. Editors of Biological Flora: A. R. Clapham, H. Godwin, P. W. Richards.
Council: H. G. Baker, A. R. Clapham, D. E. Coombe, J. B. Cragg, C. Diver, C. Elton, C. H. Gimingham, J. E. Harley, J. A. Kitching, Miss J. Lambert, E. D. LeCren, A. Macfadyen, A. J. Rutter, D. H. Valentine, M. E. Solomon, A. S. Watt.

It was pointed out that no actual retirements from the Council occurred in January 1953, it was therefore necessary to re-examine the terms of election to it. As certain aspects of the rules of the Society were to be examined by the Council during the year, it was agreed to consider this also.

Prof. G. C. Varley then brought before the Society some of the proposed changes in the rules of the Society, copies of these being circulated to members during the meeting. There was criticism of the fact that these proposed changes in rules had not been circulated with the programme. Mr Gilson, Mr Chear, Mr Davies and Dr Godwin took part in this discussion. Prof. Varley pointed out that the changes proposed were of a minor nature, removing anomalies, and clarifying them where they were difficult to interpret or in conflict with current practice.

The proposed changes were therefore accepted by the Society. The changes in rules were:

For Hon. read Honorary throughout.

Rule 3, line 3, delete the words 'or more other members' and substitute 'other member'.

Rule 4, line 2, delete the word 'minimum'.

Rule 7, line 2, delete words 'not less than'.

Rule 8, after the two existing paragraphs insert the previous rule 17 as para. 3.

Rule 9, line 7, insert the words 'President or' before the word 'Vice-President'.

Rule 13, amend to read 'The two Honorary Treasurers shall be elected for a period of three years and shall be re-eligible. The Honorary Treasurers shall keep the Society's funds and be responsible for the collection of subscriptions. Their sanction shall be required for the disbursement of the Society's moneys. The financial status and policy of the Society shall be considered each year at the meeting of Council held as soon as practicable after the audit. A financial statement shall be made to the Society at its next meeting. The audited accounts shall be published in the Journals of the Society.'

Rule 15, line 1, for 'one fortnight' read 'two weeks'; line 2, for 'members of the Society' read 'Members of the Society resident in the British Isles'.

Renumber rules 18–27 as 17–26.

Rule 19 (now 18) line 2, delete 'later'.

Rule 20 (now 19) line 3, for 'by the secretaries' read 'to the secretaries'.

Rule 21 (now 20) line 1, for 'only be made' read 'be made only'; line 2, for 'Members voting' read 'Members present and voting'.

Notes

Rule 13. The old rules expect the Treasurers to produce a financial statement at the Annual Meeting. In practice, as the bills for the year have at that time not come in, the only statement possible is very incomplete. The proposed amendment gives the Treasurers the power to present the financial statement when it is complete after audit.

Rule 20 (to be renumbered 19). The proposed change corrects what appears to have been a misprint.

All the other changes are either purely verbal or are clarifications, and remove inconsistencies in the original drafting.

Prof. Varley reported that further changes were likely to be considered by the Council during the year.

At 11 a.m. Dr C. B. Williams gave his Presidential address, the Vice-President, Dr W. B. Turrill, taking the chair.

Dr Williams dealt with the 'Statistical outlook in relation to ecology'. He first discussed the implications of the statistical approach and methods to biological problems generally. The second half of his address surveyed some of the ecological problems which had recently been studied statistically. They included: the quantitative relation between insect activity and weather conditions, the relation between insect populations and previous weather conditions, the relative abundance of species in mixed wild populations, the relative frequency of genera with different numbers of species, inter-generic competition in mixed populations, the distribution of plant species in quadrats, diversity as a measurable ecological character, the number of species in small and large areas, etc.

The afternoon session started at 2 p.m. The following papers were read:

Dr H. N. Southern: Balance of numbers in owls and small mammals.

Dr S. M. Walters and Mr C. D. Piggott: The interpretation of the discontinuous distribution of some members of the British Flora.

The meeting terminated at approximately 4.30 p.m. The President concluded the meeting by thanking all who had taken part and particularly Prof. W. H. Pearsall for his continued hospitality.

Report of the Honorary Secretaries

The thirty-ninth Annual General meeting was held in the Department of Botany, University College, Gower Street, London, on Tuesday, 6 January 1953. A soirée was held on the previous evening at 8 p.m. when numerous exhibits were set out dealing with ecological work in progress at University College, London and elsewhere.

The business meeting was held at 10 a.m. on 6 January. This was followed at 11 a.m. by Dr C. B. Williams's Presidential address on the 'Statistical outlook in ecology'. During the afternoon (2–4.30 p.m.) papers were read by H. N. Southern and S. M. Walters.

The Society is indebted to Prof. W. H. Pearsall for his continued hospitality and the excellent arrangements made for the meeting.

The Easter Meeting was held at Edinburgh (9–10 April) at the Royal Botanic Garden by courtesy of Prof. Sir William Wright Smith.

On 9 April six papers were read. In the absence of the President, Prof. A. R. Clapham took the chair. The meeting was well attended, sixty members and guests being present. The papers read were:

10 *a.m. to* 1 *p.m.*

G. K. Fraser:	Some topographical features of the Blanket Moss of the north-west of Scotland.
C. B. Goodhart:	Non-adaptive variation in a population of the snail, *Cepaea nemoralis*.
M. C. Pearson:	Some aspects of the ecology and history of Muckle Moss, Northumberland.
L. W. Poel:	Some effects of aeration on *Calluna vulgaris* and *Erica tetralix*.

2 *to* 5 *p.m.*

P. J. Newbould:	Cranes Moor—a New Forest bog.
S. Y. Barkley:	The sands of Forvie, Aberdeenshire.

At 8 p.m. on the evening of 9 April, Members of the Society were invited to a meeting of the Edinburgh Botanical Society, at which a lecture was given by Dr Peter Davis on 'Plant life in central and north-eastern Turkey', being an account of his expedition to the Anti-Taurus and Pontic-Taurus in 1952. The lecture was excellently illustrated and much enjoyed by all.

On 10 April a Symposium was held together with the Systematics Association on Infra-specific variation in relation to ecology. On this occasion the chair was taken by Dr J. W. Gregor. The meeting reviewed and discussed the recent advances in this field. The papers read were:

10 *a.m. to* 1 *p.m.*

J. Heslop-Harrison:	Ecological polymorphism in orchids.
H. G. Baker:	Ecotypes of *Geranium robertianum* and *G. purpureum*.
J. F. Hope-Simpson:	Plant variation and habitat on the chalk downs.

2 *to* 5 *p.m.*

Patricia J. Watson:	Distribution in Britain of chromosome races of *Festuca ovina*.
R. Riley:	Ecotypes of *Thlaspi alpestre*.

The Society is indebted to Sir William Wright Smith for his hospitality while at Edinburgh, and also to Dr Burtt, Dr Davis and Dr Gregor for the arrangements which they made for the meeting.

On the evening of 10 April, the Botanical Society of Edinburgh invited the Society to a soirée at the Royal Botanic Garden. The soirée was very well attended by members of the Botanical Society of Edinburgh, the Systematics Association and the British Ecological Society, about 110 persons being present. Numerous exhibits were put up by members of these Societies, the University Botany Department and the Royal Botanic Garden, Edinburgh. The evening was very successful and enjoyable. Prof. Valentine expressed the thanks of the visiting Societies to the Botanic Society of Edinburgh for arranging the soirée and for the hospitality and the very excellent refreshments provided.

The Systematics Association continued their meeting on 11 April. By invitation several members of the Society were present. Mr John Gilmour was in the Chair, and the subject of discussion was 'Taxonomic research: problems and methods suitable to Universities and the major herbaria'.

The Summer Meeting was held in perfect weather at the Malham Tarn Field Centre of the Council for the Promotion of Field Studies. It opened on the evening of Wednesday, 1 July, when the Warden, Mr P. F. Holmes, gave an interesting and useful account of the geology and topography of the Craven Pennines. On 2 July we examined limestone pavement in the vicinity of the Centre under the guidance of Mr Charles Sinker, who showed the evidence for the view that much of what is now bare pavement was still drift-covered until late in post-Glacial time. The day's excursion ended with a walk to Malham Cove, where *Polemonium coeruleum* was in full flower. On the following day the veteran naturalist, Mr Chris Cheetham, assisted by Mr Charles Sinker, led an excursion to Moughton Fell and demonstrated many of the vegetational types and rare plants of this extremely interesting hill. 4 July was devoted to visits to Colt Park Wood and Ling Ghyll Wood, near the north-eastern corner of Ingleborough, and the last day was spent on Malham Tarn Moss and on the calcareous Great Close Mire. The Society is grateful to Mr Holmes and Mr Sinker of Malham Tarn Field Centre, Prof. A. R. Clapham and to Mr Cheetham for the great trouble they took to make this an enjoyable and successful meeting.

During the year two parts of vol. 41 of the *Journal of Ecology* have appeared. Part 1 is of 206 pages, containing 14 original articles and 1 review. Part 2 has 271 pages, 16 original articles, 11 reviews, and reports of meetings for 1952–3. Two further contributions to the Biological Flora appeared:

D. N. McVean: *Alnus glutinosa* L. Caertn.
L. J. G. Dodds: *Plantago coronopus* L.

Two parts of Vol. 22 of the *Journal of Animal Ecology* have also appeared. Part 1 has 198 pages with 13 original articles, 1 review and 18 pages of abstracts of publications on the British Fauna. Part 2 has 249 pages, 12 original articles, 7 reviews and 37 pages of abstracts.

During the year there has been an increase in the membership of the Society from 768 to 792, i.e. by 24. New members have increased by 80, while 56 have ceased membership following resignation, death (7) or have ceased paying their subscription.

The Society regrets to report the death of eminent members in Miss W. E. Brenchley and Dr E. L. Praeger.

An analysis of membership is as follows:

Total	Receive E. only	Receive A. only	Receive A.+E.	Associate members	Hon. members
792	424	225	131	120	2

Distribution:	Home	572
	Abroad	220
		792

The Honorary Treasurers then gave their report, this being read by Mr V. S. Summerhayes. He reported, for the time being, the favourable position of the Society—calculating a surplus of £486*. He reported increased sales over the previous year, £1454 worth of back numbers being sold (*Ecology*, £738; *Animal Ecology*, £716).

With both *Journals* there appeared to be an even balance of sales and costs. Mr Summerhayes stressed that this was an interim account and that a final report would be given after he had received the report of the Auditors. On the motion of the Chairman this report was accepted.

Mr Le Cren proposed and Dr Hughes seconded that Messrs William Norman and Sons should be reappointed Auditors of the Society. This was accepted.

Prof. Valentine proposed, and Dr Clarke seconded, that the following grants be renewed:

The Freshwater Biological Association, £10; Co-ordinating Committee for Nature Conservation, £2. 2*s*. This was approved by the Society.

* The Hon. Treasurer now (12 February 1954) estimates this to be between £500 and £600.

The Society then proceeded to elect its new president, Prof. A. R. Clapham, and other officers and member of Council. Dr A. S. Watt, from the Chair, proposed that the Council's nominees be accepted. The Society unanimously agreed.

President: A. R. Clapham.

Vice-Presidents: J. A. Kitching, D. H. Valentine.

Hon. Secretaries: E. D. Le Cren, R. E. Hughes.

Hon. Treasurers: V. S. Summerhayes, C. E. Hubbard.

Hon. Editors: H. Godwin, H. C. Gilson.

Hon. Assistant Editor: D. E. Coombe.

Hon. Editors of Biological Flora: A. R. Clapham, H. Godwin, P. W. Richards.

Council: H. B. Hynes (1954), G. C. Varley (1954), C. B. Williams (1954), F. H. Whitehead (1954), C. Diver (1951), C. S. Elton (1953), G. H. Gimingham (1951), A. Macfadyen (1952), A. J. Rutter (1951), M. E. Solomon (1951), A. S. Watt (1952).

The date following the names of Council members refers to the year of the Annual General Meeting at which they were elected.

Dr A. S. Watt also proposed the election of three new members of the Society.

The new President then took the chair. In thanking the Society the president expressed the indebtedness of the Society for the work during the past 2 years of the retiring President, Dr C. B. Williams. The Society then proceeded to consider the reports of the Honorary Editors. The President expressed his regret that Dr Godwin owing to illness was unable to present his report.

Mr Gilson then reported on the position of the *Journal of Animal Ecology*. He mentioned the resumption of the abstracts of papers dealing with the ecology of animals in the British Isles. A year's arrears had to be made up, therefore a large number appeared during the year. These abstracts were edited by Prof. Harvey. The first part of volume 23 of the *Journal of Animal Ecology* was in the press and contained eight original papers. Mr Gilson estimated a delay of twelve months in the publication of papers and suggested that it might be found necessary to increase the size of the *Journal* to cope with the number of papers available.

Mr Gilson then proposed, and was seconded by Prof. Valentine, the renewal of a grant of £20 to Dr Hobby for checking the references included in the *Journal of Animal Ecology*.

Dr Watt commented that an increase in size of the *Journal* might mean an increase in the subscription rate.

Prof. Clapham then reported on the Biological Flora—two new accounts had appeared and a small increase was noted in the number of accounts becoming available for publication. He stressed the importance of increasing the rate at which accounts could be published.

The Society then proceeded to consider the proposed changes in rules. A draft of the new rules had been circulated to members, together with an explanation of the proposed changes. This was in accordance with the wishes of the last Annual General Meeting (6 January 1953), which were that the Council reinvestigate the rules.

The suggested new rules were based on those adopted by the Annual General Meeting of January 1949 (recorded in the *Journal of Ecology*, vol. 39, p. 187). Minor amendments to these rules were made at the General Meeting of January 1953 (*Journal of Ecology*, vol. 41, p. 423).

The changes now put forward concerned the methods of electing Council and certain officers:

(i) Rules 8*a*, 9*a*, 9*b* and 11*b* ensure that (apart from casual vacancies) there shall be 25 members of the Council, and that 4 members shall retire and 4 members shall be elected at each Annual General Meeting.

(ii) That any ordinary member of the society is eligible to the office of President or Vice-President. Rule 10*c* corresponds to existing rule 10 with the omission of the restrictive first sentence, 'The President and the two Vice-Presidents shall be nominated from among the Members of Council'.

In the draft rules, rules 1–9 correspond with existing rules 1–9. The remaining rules have been re-

numbered. In the following list the number of the draft rules is followed by the corresponding number of the existing rules in brackets:

10*a* (11);	13*a* (15);	18 (23);
10*b* (12);	13*b* (16);	19 (24);
10*c* (10 part);	14 (18);	20 (22);
10*d* (13);	15 (19);	21 (25);
11*a* (17);	16 (20);	22 (26);
11*b* new	17 (21);	23 (27).
12 (14);		

During the meeting Mr Summerhayes commented generally on the desirability of these changes. Dr Watt also mentioned that the changes in arrangements for election to the Council ensured stability and continuity, and at the same time leaving room for the election of younger members.

Prof. W. H. Pearsall proposed and Prof. Clapham seconded that these changes in rules be adopted by the Society. The Society unanimously agreed to accept their recommendation. The full text of the new rules is appended.

Dr Hughes then announced arrangements for further meetings. The Easter Meeting (2–3 April) was to be at the Botany Department, University College, Gower Street, London, by courtesy of Prof. Pearsall. The Summer meeting was to be at Aberystwyth (19–24 July) by kind invitation of Prof. Lily Newton and Prof. Stephenson.

It was also hoped that a meeting would be held at the Botany School, Cambridge, during the latter half of September.

The morning paper-reading session which commenced at 11 a.m. was devoted to a symposium on the ecology of the 'Papyrus swamps of Uganda'.

The opening contribution by Dr G. S. Carter was an account of his visit to Uganda during 1952–3. He discussed the aquatic environment of the papyrus swamps.

In Uganda and some other parts of Africa papyrus swamps cover considerable proportions of the area of the countries, either bordering lakes and rivers or filling the bottoms of valleys which may be clogged by swamps many miles long and several broad. The swamps never carry more than a poor aquatic fauna; a fauna poor both in species and individuals. Observations were made on the chemistry of the swamp waters in the neighbourhood of Jinja on the northern shore of Lake Victoria, with the object of determining the reasons for the paucity of animal life in the swamps and of comparing the conditions with those in tropical swamps in other parts of the tropics.

The littoral region of Lake Victoria shows a succession of habitats in the order: open water—lily zone—papyrus swamp—grass swamp—shore. In the lily zone the water is chemically similar to that of the open water, but the cover of leaves (about 50 % of the surface) greatly reduces wind disturbance. The water is usually stratified within the top 2 ft., and the lower layers are often deoxygenated and contain a higher CO_2 content.

In the papyrus swamp the most marked feature is a steep gradient of conditions from the lake edge to the shore. The surface water above the mat of roots formed by the papyrus at a depth of about a foot is everywhere very different from the bottom water. Within a few yards of the lake edge, mixture with water from outside the swamp renders the conditions less extreme than farther within the swamp—typical figures for surface water are; O_2 50 % saturation, pH 7·5, CO_2 4–5 p.p.m., but nearer the shore O_2 is nearly always absent even from the surface water, pH about 6·5 and CO_2 up to 40 p.p.m. There is also a marked increase in conductivity and total iron towards the shore. Below the mat conditions similar to those at the surface of the shore edge of the swamp extend to near the lake edge. Seasonal changes in the conditions, especially the effects of heavy rainfall in a wet season, were discussed. The causes of this distribution of conditions were also discussed.

In the valley swamps conditions are similar to those in the parts of the lake swamps near the shore, or are even more extreme, except in open pools.

Clearly the waters of the lake swamps are completely isolated from the open waters of the lake. All the waters of the swamps are very difficult environments for any water-respiring fauna. In their deoxygenation, high CO_2 content and acidity they resemble the waters of many other types of tropical swamp.

Dr E. M. Lind then gave her paper on the swamp floras.

Nearly 15% of the surface of Uganda is occupied by swamps which form round the lakes and also in the wide, shallow river valleys. *Cyperus papyrus* is the most widespread swamp plant up to about 6500 ft., but others are locally dominant over wide areas. *Miscanthidium violaceum* is found round some of the lakes and also alone or mixed with *Cyperus papyrus* in river valleys. It is often associated with *Sphagnum* and is rich in associated species. *Cladium jamacaense* occurs in patches in the lake swamps and covers several miles in one upland valley.

Typha sp. is often found mixed with *Cyperus papyrus* and *Miscanthidium*, but it also can form pure stands.

Phragmites sp. is a pioneer in colonizing the more silted parts of the lake edges where it forms floating mats, and is also the chief component of swamps in the district near Fort Portal characterized by the presence of volcanic ash.

Pycreus spp., *Carex* spp. and grasses are the dominant plants in swamps over 7000 ft.

Analysis of the mud shows that *Cyperus papyrus* can tolerate a wide range of pH and exchangeable calcium. *Miscanthidium* favours more acid conditions with low exchangeable calcium, while *Cladium* muds have the highest pH and exchangeable calcium.

In the Kashambye Valley in south-west Uganda areas dominated by *Typha*, *Papyrus*, *Miscanthidium* and *Cladium* succeed each other, the change from one to the other being quite abrupt. This valley may have been dammed at intervals by silting or land slides to form a chain of lakes with differing drainage. All the swamp associations exist as floating mats though the margins are occupied by papyrus.

Swamp plants are much used for building and thatching and the vegetation is subject to regular cutting and burning. It is not yet clear whether in certain conditions there is a succession from papyrus to other communities. Many swamps have no trees, probably owing to burning, but the natural succession seems to be either to *Mitrazyne*, *Phoenix* forest or to *Syzigium cordatum* forest—the latter possibly after a *Miscanthidium* stage.

Prof. L. C. Beadle then gave the last paper in the symposium, on environmental conditions in the mat below the swamp.

Except near the landward and waterside edges, a papyrus swamp usually shows little or no surface water. The plants grow from a mat of waterlogged and decomposing vegetable matter several feet thick which is usually floating on a watery layer above a substratum of peat. In heavy rain some surface flooding will occur, and in prolonged dry weather the upper surface will begin to dry out. But for most of the time it is waterlogged to the top with occasional exposed puddles of water. The chemical transformations which occur in this material are of obvious practical interest in relation to the possible exploitation of what must be regarded as a vast reservoir of plant materials.

Measurements of redox potential in the field show that, so long as there is waterlogging, the potential (E_7) is often below +100 mV. within a centimetre of the surface and approaches zero potential at 5–10 cm. In small puddles potentials of less than +200 mV. were found within 0·5 cm. of the water surfaces. There is therefore no question of any available free oxygen for respiration except in the very surface film.

Contrary to expectation, a rich invertebrate fauna was found both in the puddles and in the upper few centimetres of the waterlogged mat. In the puddles Cladocera and copepod Crustacea are often abundant, and Culicine and other dipterous larvae, nematodes and ciliate Protozoa are common. Copepods and Cladocera can be collected from the upper layers of the mat. It is difficult in the field to be certain that any of these animals is completely deprived of free oxygen, but laboratory cultures suggest that the Crustacea at least are capable of a purely anaerobic metabolism.

A most interesting and important animal is the glossoscolecid oligochaete worm *Alma emini*, which is very abundant except at high altitudes and must play the same role as the earthworm in the decomposition processes in the mat. It breathes atmospheric oxygen by exposing a short piece of its hind end

which is temporarily shaped into a tubular lung. Its haemoglobin is well adapted to the conditions of life, being extremely sensitive to oxygen and insensitive to carbon dioxide.

The remarkable ecological conditions in these swamps and the interesting flora and fauna were the subject of a very lively discussion.

Prof. Varley suggested a source of oxygen from the intercellular spaces of the roots. He also asked about the fish fauna. Dr Carter said that many were lung-fishes and noted *Tilapia* in the mud of the lily zone. Prof. Beadle also mentioned the finding of *Protopterus* amongst the stools of the papyrus. Dr E. W. Jones noted that the filling up of open water was more common in southern regions. He considered that vegetation in open water was sensitive to wind. Dr Gorham reported a similar situation in North America. Dr Watt pointed out that such conditions (papyrus swamps) did not occur in Australia.

In reply to Dr Gorham, Dr Carter noted that water draining off the land had a higher iron content. Prof. Pearsall then pointed out that the surrounding plateau was of Miocene origin. The soils were very old. He speculated on the land origin of the iron, this being precipitated in the swamps as sulphide. Under the prevailing anaerobic conditions this would be mobilized as ferrous iron.

Dr Lind referred to the possible application of pollen analysis to this study. Mr Lambert compared the general vegetational features of the swamps with those in the fens, with particular reference to the development of carr. In this connexion Prof. Pearsall mentioned two kinds of *Miscanthidium*, i.e. *Miscanthidium* leading to *Miscanthidium* with *Sphagnum*, and this to acid woodland.

In reply to Dr Gorham, Dr Lind stated that some of the *Sphagnum* species had been identified.

Others taking part in the discussion were Dr Hughes, Dr Solomon, Mr Gilson and Dr Milne-Redhead.

The afternoon session was opened by Dr J. C. Ritchie who read a paper entitled 'Observations on the distribution of *Primula scotica*'.

Attention was drawn to two of the important suggestions which have emerged from recent quaternary research: (*a*) that the disintegration and disappearance of the ice sheets of the last glaciation in Britain initiated a sequence of climatically controlled changes in substratum, from open, unstable, base-rich mineral soils which were colonized by 'Park-Tundra' vegetation and eventually replaced by leached forest-bearing soils and extensive peats; (*b*) that there is a large and increasing group of plants which are represented in Full-glacial and Late-glacial deposits by fossils which have been found in areas from which the plants are now absent. A record exists of *P. scotica* from the Cam valley, and this has been ascribed to the 'arctic beds' of the Full-glacial. It was suggested that an investigation of the present distribution of this plant in relation to its ecological amplitude and dispersal might be of value in an assessment of the environmental changes which might have effected a change in the area of the plant.

The distribution in north-west Europe of *P. farinosa* (diploid and tetraploid), *P. scotica* (hexaploid) and *P. scandinavica* (octoploid) was presented, and a complete detailed map of the distribution of *P. scotica* showed that it is restricted to Caithness, Sutherland and the Orkney Islands. It was demonstrated that the plant is confined to unshaded habitats with moderately base-rich substrata and a relatively high water-table; the main habitat types are cliff grasslands, dune 'slacks' and inland grass-heath flushes.

The results of an attempt to evaluate, by experiment, the effective seed-dispersal distance of the plant were presented and it was shown that—within the conspicuous limitations of the experiment—winds of exceptionally high speeds would be necessary to effect the transfer of seeds over distances of 5–10 km., but it was stressed that the vast majority of seeds are dispersed over distances which scarcely exceed 30–50 cm.; however, the important effects of soaring due to turbulence were recognized, and it was pointed out that no objective assessment of this is practicable. Some attempt to examine the availability of habitats to *P. scotica* was referred to, and it was suggested that very few suitable sites lie within the apparent effective dispersal distance of seeds; this is confirmed, in part, by the fact that almost all the stations for the plant have been known for at least 100 years.

The general conclusions which were suggested were that the extension of the present area of *P. scotica* is limited by the prevalence of moorland, forest (locally) and peat over much of the land which is contiguous with the present stations and the complementary limited availability of unshaded, base-rich habitats; further, the spread of the plant is limited by the method and efficiency of seed dispersal. Thus there is some accordance with the suggested requirements for the existence and spread of the plant and the conditions of habitat and vegetation which are thought to have followed the last glaciation.

In the discussion that followed Prof. Valentine questioned the reliability of the identification of macroscopic remains of *P. scotica* in the Cam valley deposits. Dr R. E. Hughes pointed out that the calcium figures given by Dr Ritchie for soils from *P. scotica* habitats were probably too low, this being due to the analytical method used (leaching soil with acetic acid, which also extracts phosphate which interferes with flame photometric determination of calcium).

There was some discussion on the mechanism of dispersal. Dr Baker referred to *P. magellanica*, which had a discontinuous distribution and he suggested other means of dispersal than wind. Dr Ritchie stressed that the evidence was in favour of short distance dispersal. Dr Varley and Dr Watt contended that experimental wind effects do not reflect conditions in the field, Dr Watt stressing the possible effectiveness of whirlwinds in long distance dispersal. Mr Le Cren pointed out that there had probably been ecotypic differentiation since glacial times.

Dr Gimingham and Dr Lambert also took part in the discussion.

Dr Whitehead then gave his paper on the ecological significance of alpine growth forms.

In a previous paper, the existence was shown of a relationship between the parameter Z_0 (which is determined from wind velocities and is a measure of the effect of surface irregularities on wind velocity profiles) and the height of vegetation on the altipiano of Monte Maiella. Further investigation showed that a similar relationship exists between Z_0 and the composition of communities there in terms of growth-form. If this correlation between surface irregularity and plant height and growth is other than fortuitous, it would be expected that alteration of the degree of surface irregularity in any one of the community types would produce a change in the vegetation. Permanent quadrats were established in 1951 and were walled around by rough stone walls, about 1 ft. in height. Records of the vegetation of these quadrats has been made each year, and although not yet fully worked out, it can be said that there has been a more than twofold increase in plant height and also changes in growth-form. Although species from other communities have not yet appeared, there have been considerable changes in the proportion of the species represented. In addition, some species have completely disappeared. It might be supposed that shading effects were operating to bring about the height differences, especially as the greatest increase, in most cases, was against the south-west wall. However, the next greatest height increase (and in some cases the maximum height increase) was against the north-west wall, so that it would appear more likely that the height increases were related to protection from exposure to a westerly wind component. It is, however, premature to ascribe these phenomena entirely to wind effects especially since, as yet, little is known of the physiological effects on plants of exposure to winds. Laboratory and further field studies are in progress to determine the causal factor or factors involved in bringing about the relationships described. It is suggested that growth-form studies may yield valuable information regarding the operation of limiting factors and the process of competition in plant communities.

Dr Gorham suggested that the plants themselves might have some influence on Z_0. In reply to Dr E. W. Jones, Dr Whitehead said that goats and sheep did graze the area for a short time. Prof. Valentine asked about winter conditions and variation in snow cover. It was pointed out that the minimum depth of snow was about a foot. Dr Gimingham stressed the importance of ecological studies of extreme habitats.

The final paper of the meeting was that of Dr J. S. Colman and Dr F. Segrove on the Tidal Plankton of a sandy beach. This was given by Dr Segrove.

The plankton of the tidal water of a small sandy beach at Robin Hood's Bay, Yorkshire, was investigated during a short period in June and July 1949. The material was collected by hauling a specially devised bottom plankton trawl, fitted with two superposed nets, in 2 ft. of water at the edge of the tide at various levels on the shore. Five series of hauls were made, one in daylight, four in the hours of darkness.

The daylight catches were poor, with the exception of the first which was taken at low tide. A possible explanation is that subtidal forms, though active in the neighbourhood of their normal habitats, are restricted in their movements in daylight.

The night catches included both intertidal sand-inhabiting forms and migrants from the subtidal zone. The numbers of the sand forms in the plankton, mainly amphipods of the genera *Bathyporeia* and *Pontocrates*, corresponded closely with their zonation in the uncovered beach. Only about $\frac{2}{3}$–1% of those

known to be present in the beach were in the plankton and they were more numerous at the bottom of the water than at the surface.

Amphipods, mysids and crab larvae were the most important migrants from the subtidal zone and reached the edge of the tide at different times. In calm conditions few species were present in appreciable numbers, but in rough conditions numbers generally increased and other species, including members of the permanent plankton, appeared. These changes may be attributed to passive transport of some species in the horizontal direction as a result of water turbulence. Mysids, however, avoided the surf and their numbers markedly decreased in rough conditions.

Comparison of the catches of the two nets showed that whilst the migrant amphipods were evenly distributed from top to bottom in 2 ft. of water, the mysids were twice as numerous towards the bottom and crab megalopas and cumaceans were twice as numerous towards the surface.

The necessity for further work was emphasized. More precise knowledge of the movements of individual species will require that hauls be taken in deeper water as well as at the edge of the tide.

At the conclusion of the session Dr A. S. Watt expressed the thanks of the Society to our hosts at Sheffield, particularly the President, Prof. A. R. Clapham.

To terminate the meeting Prof. Clapham very kindly provided us with an excellent tea at the Botanical Laboratory. The tea and discussion which ensued were thoroughly enjoyed by all.

R.E.H.

LIST OF MEMBERS (15 FEBRUARY 1954)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

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